University of Pretoria etd – Davies, R A G (1994)

**DAVIES, ROBERT A.G.**

# BLACK EAGLE *AQUILA VERREAUXII* PREDATION ON ROCK HYRAX *PROCAVIA CAPENSIS* AND OTHER PREY IN THE KAROO

**PhD** **UP** **1994**

University of Pretoria etd – Davies, R A G (1994)

# BLACK EAGLE *AQUILA VERREAUXII* PREDATION ON ROCK HYRAX *PROCAVIA CAPENSIS* AND OTHER PREY IN THE KAROO

by

**ROBERT A. G. DAVIES**

submitted in partial fulfilment of the
requirements for the degree of

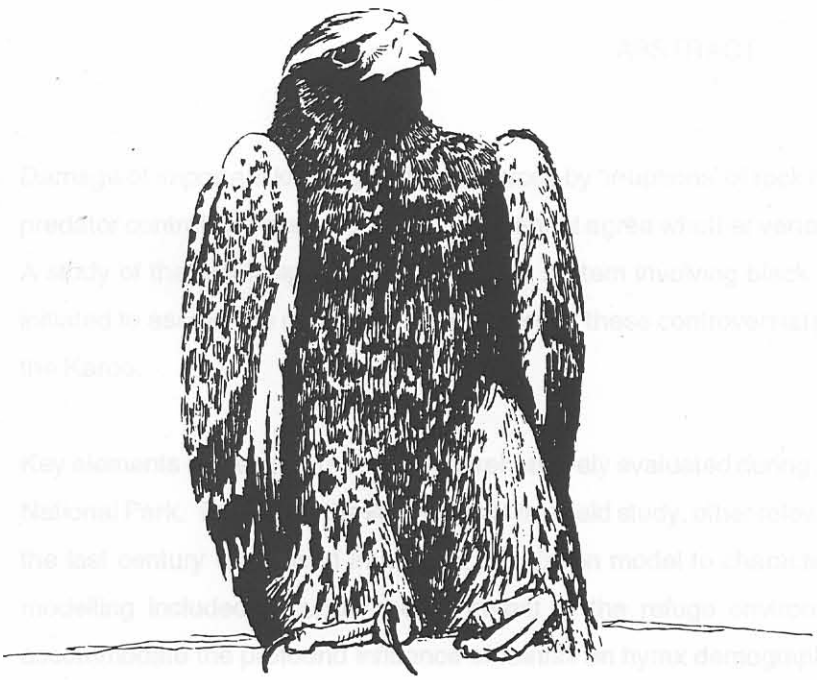
**Ph.D.**

in the Faculty of Science
UNIVERSITY OF PRETORIA
PRETORIA

**March 1994**

*to my parents, and everybody else who has helped with this*

University of Pretoria etd – Davies, R A G (1994)



*to my parents, and everybody else who has helped with this research, especially Samburu*

University of Pretoria etd – Davies, R A G (1994)



# Black eagle *Aquila verreauxii* predation on rock hyrax *Procavia capensis* and other prey in the Karoo

by

R. A. G. Davies

Supervisor: Professor J. D. Skinner
Mammal Research Institute
Department of Zoology
University of Pretoria
Pretoria

## ABSTRACT

Damage of important karoo grazing resources by 'irruptions' of rock hyrax *Procavia capensis* has been blamed on predator control, but many ecologists still cannot agree whether vertebrate predators limit/regulate vertebrate prey. A study of the highly specific predator-prey system involving black eagles *Aquila verreauxii* and rock hyrax was initiated to assess the demographic influence of these controversial predators on their prey, including livestock, in the Karoo.

Key elements in the system were comprehensively evaluated during a five year field study in and around the Karoo National Park. To escape the limitations of this field study, other relevant field research and karoo climatic data over the last century were used in a hyrax population model to characterise the long-term action of predation. This modelling included accurate measurement of the refuge environment and a simple lower trophic model to accommodate the profound influence of rainfall on hyrax demography in this water-limited environment.

The system differed from other typical predator-prey systems. Unlike cyclic prey, hyrax populations are not regularly destabilised by delayed specialist predation. They fluctuate irregularly in response to climate, but unlike other environmentally-modulated predation systems, hyrax populations do not naturally escape 'regulation' by their predators. These characteristics can be attributed to a permanent, patchy refuge resource which confers a high degree of stability on the system: hyrax are effectively protected within rocky habitat, and vulnerable to efficient predation beyond it.

University of Pretoria etd – Davies, R A G (1994)



The 'safe feeding area' available to hyrax is fixed, and was evident as a distinct vegetation zone around rock outcrops. But the number of hyrax supported within this safe habitat varies with climate, and greater protection offered to growing populations after rains is another unusual feature of this system.

Unlike sympatric generalist predators, black eagles pursued hyrax prey despite low availability. By removing a substantial number of hyrax which were otherwise unlikely to die, black eagles limited hyrax population growth during the study period, and they exerted hard selection on adult hyrax. Coevolution between eagles and hyrax was indicated from certain reciprocal behavioural and morphological traits.

The population model indicated that a recent widespread decline in hyrax populations was caused by enrichment of hyrax food supplies during the 1970's, followed by sudden, severe drought. Exhaustion of pasture in arid environments may occasionally drive hyrax from their refuge habitat, and this behaviour change was probably perceived as population increases or 'irruptions' in the past.

The model demonstrated that the full complement of predators can remove surplus hyrax not supported by the refuge habitat, and 'regulate' hyrax numbers around the number of protected prey (this number varied stochastically with climate, so the predation response was 'availability dependent' not density dependent). Intense predator control probably severely hindered the removal of surplus hyrax during the 1940's drought.

The cost of hyrax surpluses predicted in the absence of predation by black eagles outweighed the overall cost of lamb-killing by black eagles by 150 times. Tolerance of such compatible predators should help restore the ecology on karoo farmland to some of its former diversity and stability.

University of Pretoria etd – Davies, R A G (1994)



# ACKNOWLEDGEMENTS

In 1986 I approached Professor John Skinner of the Mammal Research Institute at the University of Pretoria with the idea of initiating a study on the predation of rock hyrax in the Karoo. Prof. Skinner has helped me carry out this project unfailingly ever since, by endorsing, supervising and administrating the project and by contributing financially from his own private research funds at the University. I thank him for making this research possible, and for all the advice, friendship and interest that I received from him and from his wife Patsy.

Most of the running costs of this project were covered by an extremely generous sponsorship from South African Eagle Insurance Co. Ltd., which was facilitated by Dr. John Ledger. This company has taken a very active role in eagle conservation, and they showed a particularly genuine concern that the present research should clarify the role of large eagles on farmland. I thank Fred Hasslett and Peter Martin for seeing fit to making this donation, and especially Ann Marklew for organising it all, and for the special interest that she and through her, many others at S.A. Eagle, took in Samburu's early adventures. Other financial contributors to the project were the Mammal Research Institute, the National Parks Board who sponsored the development of a geographical information system of the study area, and the African Raptor Information Centre who contributed to expenditure on one of the later field trips. I thank the Foundation for Research Development for supporting me with a doctoral bursary throughout the field work.

Many others contributed to this project by helping with equipment. Geographical Information Management Systems (GIMS) in Midrand allowed me the use of sophisticated GIS software which proved invaluable for analyses and presentation in this thesis - I especially appreciated the interest that Steve Hine, Richard Lees, Shane Clarke, Vasco Nunes, Jillian Muller & Colin Childs of GIMS showed in this particular application of their software. I also received help from GIMS and from the GIS lab at the University of Pretoria (see later) in use of the software. Other computer hardware and software used in this project were supplied at a very reduced rate by Keith Musgrave of Diginet Systems and Paul Moses of Software Connection. Climbing equipment was kindly loaned to me by Richard Wilmot, and supplied at low cost by Camp and Climb (Pty Ltd.). Kevin Deutchman at Agfa enthusiastically organised all the super-8 mm cine film for time-lapse photography at eagles' nests and this represented a huge saving. Many private cine owners let their cameras go 'for a song' for the project, including Keith Musgrave of Diginet Systems who donated many hours of his precious time to design and construct a time-lapse circuit and weather-proof housing for the cameras. The Wildlife Society of southern Africa provided a motorbike for a year. Leon Fourie allowed me the use of his hyrax traps, and Lucius Moolman (National Parks Board) and Dr. Dirk Brand (Cape Nature Conservation) helped by loaning cage traps for caracals. Dr. Neil Fairall (Cape Nature Conservation) supplied four radio collars for caracals. Gerrit van Urk and Chris Heunis of Potchefstroom University took great interest in developing a possible remote tracking system for black eagles. All who contributed with equipment expressed sincere interest in the success of the project and I thank them for that.

In the Karoo I experienced friendship and hospitality from many landowners - I am especially grateful to Richard Wilmot, Christie Mocke, Dantjie Nel, Oom Piet de Villiers, Jannie Swiegers and Danie Conroy for allowing me to study eagles on their properties and for their weakly-concealed love of these birds; and thanks to all the other farmer friends who boasted to me how many eagles they had shot today but in reality wouldn't ever dream of it. Verner and Moira Coster took such care of their eagles that it was sometimes difficult, even as an eagle biologist, to get anywhere near them! I would also like to thank those farmers who held judgement with regard to 'problem' eagles on their properties and offered me the opportunity of investigating these situations. Rory Allardice, Rob Erasmus and Dr. Morné du Plessis helped me with two such investigations. But the landowners or custodians I owe the most to are the National Parks Board for allowing me the privilege of working in the spectacular Karoo National Park, and for providing me with wonderful on-site accommodation for the first three years of fieldwork. The staff of the Karoo National Park were great to work with and all took a very active interest in this research, but I would especially like to thank the warden, Harold Braack, his wife Toni and their two sons Joe and Michael for making the park such a very fascinating and very friendly place to work in and for helping me in so many ways. I am also grateful to Nick Geldenuys, Dr. Anthony Hall-Martin, Dr. Rod Randall, Peter Retief and Francine

University of Pretoria etd – Davies, R A G (1994)


van Heerden for supporting this research in a National Park. I would also like to thank Dries Engelbrecht (current warden of the KRNP) for allowing me to complete my research, and Henriette Engelbrecht for making sure all visitors to the park learned about their raptors. For the last year of fieldwork I thank the Beaufort West Municipality for allowing me to live in the palatial departure lounge of the Beaufort West airport and for allowing Samburu to live in the control tower.

I had a tremendous amount of help with many aspects of this project, and the chapters on red rock rabbits and caracals in this thesis simply would not have been possible without field assistance. I am very grateful to Elsabe Aucamp who did most of the field work on red rock rabbits which involved arduous line transects through treacherous terrain, and many cold, dark nights chasing bunnies with spotlights, nets and sprained ankles. Richard Wilmot and Esme Loubser helped to make this fun, and Esme spent many hours looking for drollejies that glow in the dark! Dave Pepler, Andrew Duthie, Dr. Andrew McKenzie and Dr. George Ellison all helped with advice on this rabbit research. Sascha Klemm, assisted by Bennet Smith, set the cage traps for caracal in the park and diligently checked these every morning until we had captured two cats. Dr. Dirk Brand from Cape Nature Conservation provided useful advice throughout and made a special trip up to the park to help us catch two more cats. We then spent many hours walking around the park at night to try and radio-locate these animals. Colin Valet, Ken Findlay and Mike Musgrave helped us with this task. The radio-tracking was unsuccessful but I would like to thank Sascha for his efforts, for still providing very useful data on trapping success, and especially for his good company. Gus van Dyk at the Mammal Research Institute very kindly and competently analysed the prey contents of caracal scats collected in the park.

I was very fortunate to be able to call on expert advice and assistance in other crucial aspects of this research. Brigitte Randall and Katryn van Heerden helped me to conduct analyses of the vegetation zones surrounding hyrax colonies, even to the extent of counting 'dassie drollejies'. David Shearing helped us to identify the plants that we found. At the South African Museum in Cape Town Dr. Graham Avery shared his great archaeological knowledge and showed immense patience by painstakingly helping me to identify and match up literally thousands of bone fragments collected from eagle feeding sites. Esme Loubser helped me work through mountains of decomposing dassie skulls, with only occasional exclamations of disgust. Dr. Margaret Avery supplied relevant literature and also helped identify smaller prey items. Dr. André Boshoff and Guy Palmer generously allowed me access to their data and to their extensive collections of black eagle prey remains from around the Cape for the purpose of age-classification of hyrax material. Dr. J. C. Vogel of the CSIR in Pretoria determined the age of some black eagle nest material by radiocarbon dating. Drs Hector Dott and Willem Ferguson, with their great computing skills, helped take the mystery out of computer modelling for me. Willem in particular gave me an enormous amount of his precious time and thoughtfully contributed to the biological rationale of the model as well as to the workings of the program. Willem also kindly translated the summary of this thesis into Afrikaans. It was a great pleasure to work with Prof. Willem van Riet, Jan van Rensburg, Lourens du Plessis, Barend Terblanche and all the other staff of the GIS lab. at the University of Pretoria who organised the data capture for a GIS of the study area at very low cost, and who patiently helped me solve all the bugs. I would especially like to thank Jan for his time, his advice and for constructing a 'TIN' model of the KRNP (page 17), and also Stuart Slabbert and Thomas Minnie who put in the long hours digitizing contours and rock outcrops in precise detail.

In the field, I also had much help with the annual counts at hyrax colonies, especially from Marius van der Merwe and Gus van Dyk who uncomplainingly climbed mountains before dawn on many early December mornings to count the hyrax as they emerged. Esme Loubser, Mark and Tanja Anderson, Francine van Heerden, Anisca Henning, Neil and Jenny Joseph, Dr. Phil Richardson, Dr. Neil Fairall and my brother Andrew were also a great help with these counts. Another task for which I managed to enlist the help of many family and friends was the collection of prey remains from under some very inaccessible black eagle nest cliffs, and I would like to thank Andrew Davies, Colin, David, Marilyn and Ronell Forbes, Richard Wilmot, Lindy Rodwell, Mark and Tanja Anderson, Joe Braack, Jaco Loubser, David Allan, Dr. Phil Richardson, Eugene Marais, Tanja Hermann, Dr. Peter Apps, Alan Martin, Stuart Lacey and Gus Butler for all searching enthusiastically in the heat of the day for little white bone fragments on steep screes. One of the very lucky breaks in this project was finding a mountaineer, Richard Wilmot, who lived next to the park and I thank Richard for getting me safely to and from many eagle

University of Pretoria etd – Davies, R A G (1994)



nests. I also thank William Mafekiso and Jacobs Esau for providing such safe anchor lines. David Allan and Marius van der Merwe also helped scale some difficult cliffs. Trevor de Kok, Peter Steyn, Kevin Deutchman and Bob Bloomfield made useful observations from a hide at a black eagle nest. I would like to thank Mike Musgrave, Joe Braack, Bonnie Schoeman and Mark Pienaar for helping me track some elusive eagle pairs. Mannetjies Moolman and Pele Benadie took great care to monitor one important eagle nest site for me. I thank Mark Boobyer and ranger Morné du Plessis for helping with battery changes at some of the time-lapse cameras, and especially Conrad Wessels who put in very long hours peering into a cine viewer to record eagle behaviour on the nest in infinite detail.

I would like to thank the following for helping me with relevant data for the project: Dr. Alan Kemp for morphometric data on eagles; Dr. J.M. Thiollay for information on black eagle distribution; Dr. Neil Fairall for data on hyrax in the Karoo National Park prior to this research; Dr. André Boshoff, Guy Palmer, Graham Avery and M. Jarvis for access to their black eagle prey remain collections; Dr. Rod Randall and the National Parks Board for the Karoo National Park census data; the weather bureau, the National Parks Board, Jack Jonkers of the Beaufort West weather station, George Banfield, and Dr. Jeanette Lindesay of the Climatology Research Group for weather data; Louis du Pisani and Danie Olivier at Grootfontein Agricultural College, Richard Wilmot and Andrew and Danie Conroy for statistics on karoo veld and farming; Dr. Dirk Brand and Dr. Peter Norton of Cape Nature Conservation, and Jannie Swiegers for data on problem animal control; Fanie Bekker for his important findings from field necropsies on lamb carcasses; Lucius Moolman for information on caracals; Dr. Leon Fourie for information on hyrax. I would also like to specially thank Elna Randall and the Inter-Library Loans Dept. at the Merensky library for making such great efforts to acquire many obscure documents from remote corners of the globe.

This thesis has also benefited enormously from the many stimulating discussions or correspondences that I have had with Dr. Alan Kemp, Dr. Willem Ferguson, Dr. Neil Fairall, David Allan, Harold Braack, Dr. Phil Richardson, Dr. André Boshoff, Clive Webber, Dr. Graham Avery, Dr. Leon Fourie, Dr. Margaret Avery, Guy Palmer, Peter Steyn, Ken Ferguson, Dr. Peter Apps, Dr. Albert van Jaarsveld, Dr. Pieter Botha, George Banfield, Dr. Rod Randall, Arthur Bowland and most especially Val Gargett who shared her great knowledge of black eagles with me, unselfishly, right from the start. I'd also like to thank Val and her publisher, Eleanor-Mary Cadell of Acorn books, for granting me permission to use the sketches from 'The Black Eagle' to illustrate this thesis. Anseri Swanepoel helped by scanning many of the figures for me. Dr. André Boshoff and Clive Webber kindly took the time to comment on early drafts of certain chapters. Dr. Rudi van Aarde, Dr. Andrew McKenzie, Dr. Rafi Ben Shahar and Johan van Jaarsveld freely offered their advice on certain aspects of methodology. I would like to thank them all for helping me to unravel some of the secrets of this predator-prey system.

I am grateful to the Transvaal Provincial Administration for allowing me to remove an eaglet from a nest in which siblicide was occurring, and to the National Parks board for kindly permitting me to keep 'Samburu' in the Karoo National Park. The experience of raising and releasing this bird gave me an understanding of black eagles that I could not have gained any other way. I also owe a great deal of my happiness while staying in the park to Samburu. I would like to thank Hendrick de Bruin, Simon Bilikwa, Joe Braack, Mike Braack (sorry about the boot), Toni Braack (sorry about the tourists), Sascha Klemm, and Jaco Loubser for the great care they took of Samburu when I was away. John Varty (sorry about the scratch) contributed to Samburu's keep. The marksmanship skills of Joe Braack and Pieter Ryan supplied Samburu and myself with dassie material. That leaves Pat Wolfe and Piet Otto to thank for getting me airborne with the eagles, and Popaye Nteyi for brightening every day and teaching me Xhosa. There are still many things that I need to thank Esme Loubser, Harold, Toni, Joe and Michael Braack, and Richard Wilmot for, but I'd just like to thank them finally for all the fun and friendship, and Esme for all her warmth and laughter.

But the two I need to thank the most are my parents, Alan and Marilyn Davies, who are really the major sponsors behind this project. I would like to thank them both, from my heart, for all the encouragement and support that they have provided every single small step along the way, and for taking such a wonderful interest in what I was doing. I hope that they, and everybody else who has assisted with this project, have shared some of the great pleasure that it has given me, and that this 'team effort' will be of future value, both to eagles and to people.

University of Pretoria etd – Davies, R A G (1994)



# CONTENTS

Page

ABSTRACT ..... i
ACKNOWLEDGEMENTS ..... iii
CONTENTS ..... vi
LIST OF TABLES ..... xii
LIST OF FIGURES ..... xiv

*general introduction*

**CHAPTER 1: INTRODUCTION AND GENERAL APPROACH** ..... 1

*environment and the refuge resource*

**CHAPTER 2: THE STUDY ENVIRONMENT** .....
*Karoo* ..... 7
*Karoo farming* ..... 11
*Karoo National Park* ..... 14
*Period of study* ..... 19
*Previous relevant research* ..... 21

**CHAPTER 3: THE REFUGE RESOURCE** .....
INTRODUCTION ..... 24
METHODS ..... 27
*Categorization of refuge habitats* ..... 27
*Habitat mapping* ..... 28
RESULTS AND DISCUSSION .....
*Extent and distribution of refuge microhabitats* ..... 31
*Habitat suitability* ..... 34

*the prey base*

**CHAPTER 4: ROCK HYRAX DEMOGRAPHY AND BEHAVIOUR** .....
INTRODUCTION ..... 37
METHODS .....
*Annual census at hyrax colonies* ..... 38
*Estimating hyrax density* ..... 39
*Measuring group spacing* ..... 39
*Destructive sampling* ..... 40
*Behavioural observations* ..... 40
*Vegetation analyses* ..... 40
RESULTS ..... 41
*Habitat use* ..... 43
*Factors influencing the use of slopes* ..... 45
*Group size* ..... 46
*Influence of habitat on group size* ..... 46
*Group spacing* ..... 47
*Population estimates, density and biomass* ..... 47
*Poulation composition* ..... 48
*Behavioural observations and vegetation zones* ..... 53

University of Pretoria etd – Davies, R A G (1994)



Page

DISCUSSION .....

*Distribution and the use of refuge habitats* ..... 58
*Demography* ..... 60
*Behaviour* ..... 63
*The link between caverniculous and gregarious behaviour* ..... 64

**CHAPTER 5: DISTRIBUTION AND ABUNDANCE OF ALTERNATE PREY** .....

**PART 1. RED ROCK RABBITS** .....

INTRODUCTION ..... 66
METHODS ..... 67
RESULTS .....

*Appraisal of the major topographical habitats* ..... 69
*Density of middens in the major topographical habitats* ..... 69
*Smaller-scale habitat preference* ..... 71
*Distribution of middens at Mountain View* ..... 72
*Faecal accumulation rate* ..... 72
*Recovery of faecal pellets marked with fluourescent pigments* ..... 72
*Energy content of faecal pellets* ..... 72

DISCUSSION AND POPULATION ESTIMATE .....

*Middens as indicators of habitat preference* ..... 73
*Middens as indicators of rabbit abundance* ..... 74
*Middens as indicators of territoriality* ..... 76

**PART 2. NOTES ON OTHER POTENTIAL PREY SPECIES** ..... 78

*the predator guild*

**CHAPTER 6: BLACK EAGLE DEMOGRAPHY AND BEHAVIOUR** .....

INTRODUCTION ..... 82
METHODS .....

*Location and identification of nesting pairs of black eagles* ..... 84
*Nest-site selection and spacing between pairs* ..... 84
*Calculating population density* ..... 85
*Assessing breeding performance* ..... 85
*Behavioural observations* ..... 86

RESULTS .....

*Density of resident pairs* ..... 88
*Size of the breeding population* ..... 89
*Inferences on the non-breeding population* ..... 89
*Nest spacing* ..... 90
*Nest-site selection* ..... 90
*Breeding season* ..... 91
*Breeding success* ..... 92
*Behaviour* .....

*Time budgets and activity rhythms* ..... 95
*Use of habitats* ..... 96
*Flight speeds* ..... 97
*Territorial overlap* ..... 97
*Territorial behaviour* ..... 99
*A comparison of territories* ..... 100

University of Pretoria etd – Davies, R A G (1994)



Page

*Strikes at prey* ..... 101
*Surprise attacks* ..... 101
*Still hunting vs. Active hunting* ..... 102
*Co-operative hunting behaviour* ..... 102
*Movements of male, female and juvenile black eagles within their territory* ..... 103
*Morphometrics of male, female and juvenile black eagles* ..... 104
*The influence of season on black eagle behaviour* ..... 106
*Short-term influences on black eagle behaviour* ..... 108
DISCUSSION .....
*Distribution and abundance* ..... 111
*Choice of nest-site* ..... 114
*Breeding success* ..... 115
*Use of space and territoriality* ..... 118
*Foraging behaviour and success* ..... 121
*The size and shape of black eagles* ..... 125

**CHAPTER 7: DISTRIBUTION, ABUNDANCE AND FEEDING HABITS OF CARACALS AND OTHER PREDATORS** .....
INTRODUCTION ..... 128
METHODS ..... 130
RESULTS .....
*Trapping success and radio-tracking of caracals* ..... 132
*Relative abundance of other predators* ..... 133
*Feeding habits* ..... 134
*Habitat selection* ..... 135
DISCUSSION .....
*Feeding habits* ..... 138
*Abundance* ..... 140
*Habitat selection* ..... 141
*Capacity for population change* ..... 142
*Food requirements of the caracal population* ..... 142
*The potential impact of generalist predators on hyrax numbers* ..... 143
CONCLUSION ..... 145

*predator-prey interaction*

**CHAPTER 8: BLACK EAGLE FEEDING HABITS 1. PREY CAPTURE RATE** .....
INTRODUCTION ..... 146
METHODS .....
*Time-lapse photography* ..... 147
*Direct observations* ..... 149
*Food requirements of a hand-fed eagle* ..... 149
*Metabolic predictions* ..... 150
RESULTS AND DISCUSSION .....
*A test of the effectiveness of monitoring nests by time-lapse photography* ..... 151
*Observations on field predation rate and biomass captured* ..... 152
*Food consumption and energetic considerations* ..... 155
*Factors influencing prey capture rate by black eagles* ..... 162
CONCLUSION ..... 174

University of Pretoria etd – Davies, R A G (1994)



Page

**CHAPTER 9: BLACK EAGLE FEEDING HABITS 2. COMPOSITION OF PREY SPECIES IN THE DIET** .....

INTRODUCTION ..... 175

METHODS .....

*The collection of prey remains from eagle nest cliffs* ..... 177

*Direct observation of prey on the nests* ..... 180

*Direct observation of hunting and feeding behaviour of the eagles* ..... 180

RESULTS AND DISCUSSION .....

*Factors influencing the collections of prey remains* ..... 181

*Species composition of black eagle diet as indicated by prey remains in terms of numbers* ... 182

*Species composition of black eagle diet as indicated by prey remains in terms of mass* ..... 184

*Species composition of black eagle diet as indicated by time-lapse photography at nests* ..... 187

*Species composition of black eagle diet as indicated by direct observations of eagles and prey on their nests* ..... 188

*Comparisons of methods* ..... 190

*Interpolation of diet* ..... 192

*Species composition of black eagle prey in relation to availability* ..... 194

*Temporal variation in black eagle diet* ..... 198

*Geographical variation in black eagle diet* ..... 200

*The black eagle as a specialist predator* ..... 203

**CHAPTER 10: BLACK EAGLE FEEDING HABITS 3. COMPOSITION OF HYRAX POPULATION CLASSES IN THE DIET** .....

INTRODUCTION ..... 205

METHODS ..... 206

RESULTS AND DISCUSSION .....

*Overall composition of rock hyrax captured* ..... 210

*Black eagle selection of rock hyrax by age and sex, in relation to availability* ..... 212

*Annual variation in the age and sex composition of rock hyrax captured by black eagles* ..... 219

*Geographical variation in the age and sex composition of rock hyrax captured by black eagles within the study area* ..... 223

*Regional variation in the age and sex composition of rock hyrax captured by black eagles* .... 224

**CHAPTER 11: LIVESTOCK PREDATION BY BLACK EAGLES IN THE KAROO** .....

INTRODUCTION ..... 229

METHODS ..... 233

RESULTS AND DISCUSSION .....

*Nest-based investigations of stock predation by eagles* ..... 234

*Direct observations* ..... 235

*Attitudes of farmers to eagles* ..... 237

*Farmers' reports of stock losses to eagles* ..... 238

*Field necropsies* ..... 241

*Economics of livestock predation by black eagles in the Karoo* ..... 246

*Managing problem situations* ..... 247

CONCLUSION ..... 252

University of Pretoria etd – Davies, R A G (1994)



Page

**CHAPTER 12: BLACK EAGLE PREDATION AS A FACTOR INFLUENCING ROCK HYRAX POPULATIONS** .....

INTRODUCTION ..... 253

**PART 1. THE IMMEDIATE INFLUENCE OF PREDATION BY BLACK EAGLES ON ROCK HYRAX DEMOGRAPHY DURING THE STUDY PERIOD** .....

METHODS (part 1) .....

*Immediate demographic effect of predation by black eagles on rock hyrax* ..... 258

*Other factors* ..... 258

*Interactive effects of demographic factors* ..... 259

RESULTS AND DISCUSSION (part 1) .....

*The impact of predation by black eagles in relation to hyrax standing crop* ..... 260

*The impact of predation by black eagles on other prey species* ..... 261

*The impact of predation by black eagles in relation to hyrax mortality* ..... 263

*The impact of predation by black eagles in relation to hyrax recruitment* ..... 263

*The impact of predation by generalist predators on rock hyrax during the study period* ..... 265

*The influence of non-predatory mortality on the hyrax population* ..... 266

*The influence of variable recruitment on the hyrax population* ..... 267

*Inter-annual variation of demographic factors affecting the hyrax population* ..... 268

**PART 2. THEORETICAL PREDICTIONS ON THE LONG-TERM ACTION OF PREDATION BY BLACK EAGLES ON ROCK HYRAX POPULATION DENSITY IN THE KAROO** .....

METHODS (part 2) .....

*FORMULATION OF THE HYRAX POPULATION MODEL* .....

*Population composition and age-specific rates of mortality and fecundity* ..... 272

*Carrying capacity in a standard year* ..... 273

*Interpolating mortality and fecundity on P:K ratio* ..... 273

*A dynamic measure of carrying capacity* ..... 275

*Lower trophic interaction between vegetation, rainfall and hyrax* ..... 276

*Pre-natal mortality* ..... 279

*Removals by black eagles* ..... 280

*Compensatory mortality* ..... 281

*Removals by caracals* ..... 282

*Predator impedence* ..... 283

*Estimating the cost of hyrax vegetation impact to karoo farmers* ..... 283

RESULTS AND DISCUSSION (part 2) .....

*PREDICTIONS OF THE MODEL* .....

*A standard run with predators present* ..... 285

*Linking conception rates to rainfall patterns* ..... 287

*The potential influence of a bias in recruitment of the sexes* ..... 288

*Age-selective predation by black eagles* ..... 288

*Simulated removal of eagles* ..... 289

*Predation potential of caracals* ..... 291

*The demand for alternate prey* ..... 292

*Impeding both predators* ..... 293

*Contrasting the respective influences of black eagles and caracals* ..... 295

*ASSESSMENT OF THE MODEL* .....

*Fit to hyrax census data* ..... 296

*Different rainfall regimes* ..... 297

*Sensitivity analysis* ..... 299

CONCLUSIONS FROM THE MODEL ..... 302

University of Pretoria etd – Davies, R A G (1994)



Page

**SYNTHESIS AND CONCLUSION** .....

*The system under investigation* ..... 306
*Links between the lifestyles of black eagles and rock hyrax* ..... 310
*Do black eagles limit rock hyrax populations in the Karoo?* ..... 314
*Were rock hyrax 'irruptions' in southern Africa caused by the removal of predators?* ..... 315
*Do black eagles regulate rock hyrax populations in the Karoo?* ..... 317
*Do black eagles kill domestic livestock in the Karoo?*
*and if so what steps can be taken to prevent this?* ..... 320
*The role of black eagles on karoo farmland* ..... 321

**SUMMARY** ..... 324

**OPSOMMING** ..... 330

**REFERENCES** ..... 336

**APPENDICES** .....

APPX. 1. *Detailed map of the Karoo National Park and environs* ..... 352
APPX. 2. *Species names of animals referred to in the thesis* ..... 353
APPX. 3. *Breeding histories of black eagle pairs in the Karoo National Park* ..... 355
APPX. 4. *Details recorded for each caracal trapped* ..... 356
APPX. 5. *Circuit diagram for the time-lapse circuit*
*and a plot of the regression of time interval on variable resistance* ..... 357
APPX. 6. *Age-specific fecundity and mortality data used in the hyrax population model* ..... 358
APPX. 7. *A statistical summary of rainfall data used in the hyrax population model* ..... 358
APPX. 8. *Preference ratings for selection of hyrax age-classes by black eagles* ..... 359
APPX. 9. *Age-specific data on 'non-eagle' mortality used in the hyrax population model* ..... 359
APPX. 10. *Transcript of the hyrax population model (TURBO PASCALL v. 7.0)* ..... 360
APPX. 11. *Names and addresses of all persons cited 'pers. comm.' or 'in litt.' in text* ..... 366

University of Pretoria etd – Davies, R A G (1994)



# LIST OF TABLES


Page

Table 1. Ecological physiognomy of the major topographical habitats within the KRNP ..... 20

Table 2. Attributes of the principal refuge micro-habitats available to rock hyrax in the Karoo National Park ..... 35

Table 3. Analysis of hyrax habitat preferences ..... 44

Table 4. Density and biomass of rock hyrax in the major topographical habitats and a population estimate for the Karoo National Park ..... 48

Table 5. Results of the annual hyrax counts ..... 49

Table 6. Data derived from destructive sampling of rock hyrax ..... 50

Table 7. A description of the micro-habitat variables that were visually assessed for each red rock rabbit midden and at regular intervals along each transect line ..... 67

Table 8. Number of red rock rabbit middens encountered and their average perpendicular distances from line transects completed in the major topographical habitats ..... 70

Table 9. Estimates of red rock rabbit midden density in the major topographical habitats of the Karoo National Park, derived from two methods ..... 70

Table 10. Population estimate for red rock rabbits in the various major habitats of the Karoo National Park ..... 76

Table 11. Incidental observations of potential prey species in the Karoo National Park ..... 78

Table 12. Population estimates for various potential prey species in the Karoo National Park ..... 79

Table 13. Distribution of potential prey species within the major habitats of the Karoo National Park ..... 80

Table 14. A comparison of four eagle territories in terms of habitats and prey base ..... 100

Table 15. Success of black eagle strikes at prey: still hunting vs. active hunting; and solo hunts vs. tandem hunts 102

Table 16. Nest-spacing and density of black eagles in this and other studies ..... 112

Table 17. Frequency of occurrence of prey in 100 caracal scats ..... 134

Table 18. Composition of caracal diet in various regions of the Cape ..... 138

Table 19. Trapping success rates and home range estimates for caracal in various regions of the Cape ..... 140

Table 20. Annual prey capture rates by black eagles indicated by time-lapse photography at nests ..... 152

Table 21. Prey capture rates by black eagles indicated by direct observation of the birds and their nests ..... 152

Table 22. Present findings on the prey capture rate by karoo black eagles compared with other similar studies ... 154

Table 23. Results of three feeding trials on a hand-fed nestling black eagle ..... 156

Table 24. Dry matter concentration and energy content of foodstuffs used and excreta produced in feeding trials of a hand-fed nestling black eagle ..... 156

Table 25. Daily food and energy consumption of eagles on various diets in this and other studies ..... 158

Table 26. Maximum size records for prey killed by eagles ..... 178

Table 27. Size and distribution of annual collections of prey remains ..... 181

University of Pretoria etd – Davies, R A G (1994)



Page


Table 28. Composition of the entire collection of prey remains collected beneath black eagle nest sites in and around the KRNP ..... 183

Table 29. Composition of black eagle diet in terms of mass and the juvenile prey component, as indicated by prey remains ..... 185

Table 30. Composition of the principal prey taxa in black eagle diet in terms of mass and numbers, as indicated by prey remains ..... 186

Table 31. Composition of black eagle diet in terms of mass and numbers, as indicated by time-lapse photography at nests ..... 188

Table 32. Composition of black eagle diet as indicated by direct observations and nest remains ..... 189

Table 33. Prey composition of black eagle diet in terms of mass and numbers as determined by interpolation of methods ..... 193

Table 34. Prey taken by black eagles in relation to estimates of their availability and abundance ..... 195

Table 35. Composition by age and sex for all hyrax skulls/maxillae collected beneath black eagle nesting sites in and around the KRNP during the study period ..... 210

Table 36. Mean mass and frequency of the hyrax age classes represented in the prey remains ..... 211

Table 37. Pre-disposing conditions for the simulation of an hypothetical rock hyrax population - the source of their observation, and the degree to which they could be satisfied in the model ..... 213

Table 38. Findings on the predation and neonatal mortality of lambs from questionnaire surveys of ranchers ..... 240

Table 39. Findings on the predation and neonatal mortality of lambs from animal damage claims and miscellaneous incidents ..... 240

Table 40. Findings on the predation and neonatal mortality of lambs from field necropsy surveys ..... 243

Table 41. A summary of the numbers and annual mortality of small livestock in the Karoo and on the average farm for calculating the economic significance of predation ..... 247

Table 42. Annual estimates of prey available and prey captured in an average eagle territory during the study period ..... 260

Table 43. Predation impact studies of vertebrate predators upon vertebrate prey - in terms of the proportion of standing crop removed over varying time periods ..... 262

Table 44. Predation impact studies of vertebrate predators upon vertebrate prey - in terms of the proportion of prey mortality accounted for by predators ..... 264

Table 45. Predation impact studies of vertebrate predators upon vertebrate prey - in terms of the proportion of juvenile elements removed by predators ..... 264

Table 46. Annual loss and addition of individuals to the hyrax population due to various causes, expressed as proportions of population size at the start of each year ..... 269

Table 47. Key-factors analysis performed on the inter-annual variation of certain factors involved with hyrax demography ..... 269

Table 48. The results of a sensitivity analysis performed on the main predictions of the hyrax population model ... 300

University of Pretoria etd – Davies, R A G (1994)



# LIST OF FIGURES


Page

Figure 1. Distribution patterns of mountains, rock hyrax and black eagles in Africa ..... 1

Figure 2. The interaction of rock hyrax, black eagles and domestic livestock in the Karoo ..... 4

Figure 3. Distribution of mountains, Nama-Karoo and Succulent Karoo in southern Africa (rainfall regions and places referred to in this thesis are also shown) ..... 8

Figure 4. The Karoo National Park (KRNP) at Beaufort West and the major topographical habitats that it encompasses ..... 16

Figure 5. Cross-section through the Nuweveldberg in the KRNP showing the underlying geology responsible for the topography ..... 16

Figure 6. A perspective view over the KRNP looking north-west, clearly showing the eroded, plateau topography and the river incision into the lower escarpment (TIN model using ARCINFO) ..... 17

Figure 7. Prevailing wind sources in the KRNP during the field study ..... 18

Figure 8. Frequency histogram of day types recorded in the KRNP during the field study in terms of three important weather variables ..... 18

Figure 9. Seasonality of rainfall in the KRNP. Monthly rainfall averages at Stolshoek determined for the period 1911 - 1982 ..... 18

Figure 10. Annual rainfall (January to December) recorded at Stolshoek between 1972 and 1992 ..... 19

Figure 11. Monthly rainfall recorded at Stolshoek over the study period ..... 21

Figure 12. A chronological plan of the study ..... 22

Figure 13. Number of hyrax counted at two colonies in the KRNP (prior to this study) by Fairall (*in litt.*) ..... 21

Figure 14. A detailed topographical diagram of the KRNP illustrating the classes of refuge micro-habitats available to rock hyrax, and the substrates from which they derive ..... 27

Figure 15. The area within the Karoo National Park where detailed habitat mapping was conducted and its subdivision into slopes ..... 29

Figure 16. Geographical information system of the principal refuge micro-habitats within the Karoo National Park . 32

Figure 17. Routes of the episodic water courses in the Karoo National Park shown against the major topographical habitats within the mapped area ..... 33

Figure 18. Densities of the principal refuge micro-habitats in the major topographical habitats of the Karoo National Park ..... 31

Figure 19. Total extent of refuge micro-habitats within the 139km$^2$ mapped area ..... 34

Figure 20. The three age classes of rock hyrax discernible during counts conducted in December (@ one month after the birth-pulse) in the KRNP ..... 38

Figure 21. Map showing the distribution of hyrax groups in relation to the refuge micro-habitats of the KRNP ..... 41

Figure 22. Map showing the distribution of hyrax groups in relation to the episodic water courses of the KRNP ..... 42

Figure 23. Histogram showing the frequencies of hyrax groups within the various classes of refuge micro-habitats in the KRNP ..... 43

University of Pretoria etd – Davies, R A G (1994)



Page

Figure 24. An indication of the age distribution of the rock hyrax population in the KRNP (1989-1990) derived from age-determination of 52 hyrax shot ..... 51

Figure 25a. Frequency distribution of birth dates estimated for a sample of 52 hyrax shot (1989-1990); and the percentage of each cohort comprised by males ..... 51

Figure 25b. Total annual rainfall for the KRNP 1976 - 1990 ..... 51

Figure 26. An indication of the mortality rate affecting age classes of rock hyrax in the KRNP, derived from age-determination of 54 hyrax skulls collected away from known predator feeding sites ... 52

Figure 27. Map showing the total foraging ranges of four chosen hyrax study groups in the Stolshoek region of the KRNP ..... 53

Figure 28. The relationship between group size and foraging range for four hyrax study groups ..... 53

Figure 29. Daily time budget for rock hyrax derived from three 5-day periods of observation at study colonies ..... 54

Figure 30. Summer and winter daily rhythms of hyrax foraging movements and activity ..... 54

Figure 31. Total daily foraging ranges of a hyrax group over five consecutive days in August 1987, superimposed onto an aerial photograph showing rocks and vegetation ..... 55

Figure 32. Average distance ventured from shelter for three groups over five days each, in relation to rainfall experienced over the past two months ..... 55

Figure 33. The amount of time that hyrax spend at varying distances from shelter during the daytime when visible 56

Figure 34. Change in the amount of grasses at increasing distance from a regular hyrax colony ..... 57

Figure 35. Change in the amount of *Hermannia burkei* at increasing distance from a regular hyrax colony ..... 57

Figure 36. Change in the number of plants and the number of species per quadrat at increasing distance from a regular hyrax colony ..... 57

Figure 37. Change in the number of hyrax faeces and the index of cropped shoots per quadrat at increasing distance from a regular hyrax colony ..... 57

Figure 38. Model of how hyrax travel costs and the amount of accessible vegetation (food) would be expected to change at increasing distance from a regular hyrax colony ..... 64

Figure 39. Frequency histogram showing the number of red rock rabbit middens detected at varying distance categories from the transect line ..... 69

Figure 40. Population change of various species in the KRNP over the study period, in relation to rainfall ..... 81

Figure 41. The nesting distribution of eagle pairs in and around the KRNP ..... 88

Figure 42. The use of different cliff substrates for nest sites, in relation to the availability of those substrates ..... 90

Figure 43. The use of different cliff aspects for nest sites, in relation to the availability of those aspects ..... 91

Figure 44. Breeding seasonality of black eagles in the Nuweveld Mountains during the present study ..... 92

Figure 45. Percentage of lower escarpment black eagle pairs attempting to breed and successfully breeding for each year of fieldwork, in relation to changes in the prey base and rainfall patterns ..... 93

Figure 46. Relative duration of different flight styles used by black eagles ..... 95

University of Pretoria etd – Davies, R A G (1994)



Page

Figure 47. Overall daily activity rhythm of black eagles ..... 95

Figure 48. Flight paths of four adjacent pairs of black eagles in the KRNP ..... 96

Figure 49. Frequency histogram of overall travel speeds calculated for all black eagle flights lasting longer than 1 min ..... 97

Figure 50. All flight paths of the Penberi eagles when their primary motive could be identified as (A) directional flight, (B) foraging behaviour, and (C) territorial behaviour ..... 98

Figure 51. All flight paths of the Penberi eagles separated for tandem flights, solo flights by the male, solo flights by the female, and solo flights by the juvenile ..... 103

Figure 52. Differences in the flight patterns of adult male and female, and juvenile black eagles ..... 104

Figure 53. Average male and female foot dimensions, and mean body mass, for five species of *Aquila* eagles ..... 105

Figure 54. Daily rhythm in the hunting activity of black eagles during summer and winter ..... 106

Figure 55. All flight paths of the Penberi eagles for the four major periods in a black eagle's year: pre-breeding, incubation, nestling and post-fledging ..... 107

Figure 56. Flight paths of the Kortkloof eagles on two still, and two windy days ..... 108

Figure 57. Flight paths of all eagle pairs for different wind directions, when wind speed was greater than $2msec^{-1}$ 109

Figure 58. Seasonal synchronicity in the daily foraging behaviour of black eagles and rock hyrax ..... 122

Figure 59. Records of the number of caracals killed in control operations on the farm Montana, near Victoria West, in relation to rainfall patterns ..... 132

Figure 60. Relative abundance of terrestrial (A) and avian (B) predators in the KRNP, as indicated by incidental sightings during fieldwork, in relation to body mass ..... 133

Figure 61. Proportional recovery of all caracal scats from the major topographical habitats in the KRNP, in relation to the proportional extent of those habitats within the park ..... 135

Figure 62. Proportional recovery of caracal scats during field transects conducted through the major topographical habitats in the KRNP, in relation to proportional sampling effort in those habitats ..... 135

Figure 63. The distribution of caracal scats, sightings and trap localities within the KRNP, in relation to episodic drainage routes, mountain slopes and escarpment ..... 136

Figure 64. Mass gain and food consumption of a hand-fed juvenile black eagle during the 'dependent' period ..... 157

Figure 65. Frequency distributions of intervals between prey deliveries at all nests for the three years monitored .. 164

Figure 66. Percentage nest attendancy by any adults in relation to nestling age ..... 166

Figure 67. Delivery rates of hyrax and other prey for each of the 10 nestling periods which afforded sufficient data . 167

Figure 68. Change in overall prey delivery rate with nestling age, in relation to nest attendancy by adults and food need of the nestlings ..... 166

Figure 69. Overall delivery rates of hyrax, red rock rabbits and other prey to black eagle nests on different types of days (days were classified as above or below average for three important climatic variables) .. 169

Figure 70. Prey delivery rates to black eagle nests for days of different wind directions ..... 170

University of Pretoria etd – Davies, R A G (1994)



Page

Figure 71. Prey delivery rate to black eagle nests for the three nesting seasons monitored, in relation to the timing and magnitude of any rainfall events ..... 171

Figure 72. Frequency distribution of all prey deliveries (n=293) to black eagle nests throughout the daylight period 172

Figure 73. Frequency distribution of hyrax, red rock rabbit and other prey deliveries to black eagle nests throughout the daylight period ..... 173

Figure 74. Frequency distribution of hyrax deliveries to black eagle nests through the daylight period for late winter and early summer ..... 174

Figure 75. Recovery of prey items on consecutive collections from nest cliffs ..... 181

Figure 76. Relationship between the size of the collection of prey remains, and the number of species represented 182

Figure 77. Change in the percent contribution by rock hyrax to consecutive collections of prey remains ..... 182

Figure 78. Frequency distribution of hyrax and other black eagle prey in accordance with size category, as indicated from 3589 prey remains ..... 184

Figure 79. Percent composition of the principal prey taxa in black eagle diet in terms of frequency and biomass, as indicated by prey remains ..... 186

Figure 80. Percent composition of the principal prey taxa in black eagle diet in terms of frequency and biomass, as indicated by time-lapse photography at nests ..... 187

Figure 81. Direct comparison of diet composition (principal prey taxa) as determined for ten separate nestling periods using two methods: time-lapse photography at nests, and the subsequent collection of prey remains ..... 190

Figure 82. Direct comparison of diet composition (principal prey taxa) as determined by four methods: collection of prey remains; time-lapse photography at nests; observations of prey on nests; and kills and other direct observations of eagles feeding ..... 191

Figure 83. Change in percentage composition of black eagle diet over the study period, as indicated by time-lapse photography at nests, and the collection of prey remains ..... 198

Figure 84. Changes in the percentage contribution of red rock rabbits to prey abundance and to eagle diet over the study period ..... 199

Figure 85. Differences in the composition of the major prey taxa represented in collections of prey remains from beneath upper escarpment and lower escarpment black eagle nest sites ..... 201

Figure 86. Differences in the composition of the major prey taxa represented in collections of prey remains from beneath black eagle nest sites on farm and park land ..... 202

Figure 87. Sexual dimorphism evident in the upper incisors of adult rock hyrax ..... 206

Figure 88. Age-specific patterns of tooth wear for rock hyrax maxillae, from Fourie (1983: Fig. 35) ..... 207

Figure 89. Population structure of all classifiable hyrax skulls/maxillae (n=3077) collected beneath black eagle nesting sites in and around the KRNP during the study period ..... 210

Figure 90. Population structure of all fresh (category A) classifiable hyrax skulls/maxillae (n=1302) collected beneath black eagle nesting sites in and around the KRNP during the study period ..... 210

Figure 91. Percent frequency representation of the annual age classes by freshly-killed (category A) and older (categories B & C) hyrax skulls/maxillae from one large collection of prey remains from black eagle nesting sites in and around the KRNP at the end of 1987 ..... 211

University of Pretoria etd – Davies, R A G (1994)



Page

Figure 92. A diagrammatic summary of age- and sex-specific predation by black eagles in relation to the availability and the annual mortality of the hyrax population classes ..... 214

Figure 93. Preference ratings by black eagles for male and female hyrax age classes ..... 216

Figure 94. The estimated proportion of each hyrax population class removed annually by black eagles during the study period ..... 216

Figure 95. The estimated proportion of mortality affecting each hyrax population class annually, that can be attributed to predation by black eagles ..... 216

Figure 96. Change in the population composition of hyrax captured and eaten by black eagles between 1986 and 1990, as indicated by all skulls/maxillae collected beneath nesting sites ..... 219

Figure 97. Year to year changes in the composition of the major hyrax population components available to the eagles and taken by the eagles, over the study period ..... 219

Figure 98. Annual change in the percentage of hyrax crania opened by upper and lower escarpment eagles, concurrent change in the juvenile component of hyrax captured, and changes in hyrax abundance ..... 220

Figure 99. Observed and expected frequencies and sex ratio of hyrax cohorts in the prey remains collections, in relation to rainfall patterns at the time of their birth ..... 222

Figure 100. Population structure diagrams derived from rock hyrax skulls/maxillae collected beneath black eagle nesting sites for various regions in the Cape Province ..... 224

Figure 101. Variation in the major hyrax population components captured by black eagles in the eastern Cape and the Fynbos across two decades ..... 225

Figure 102. Variation in the size of adult male hyrax maxillae from black eagle prey remains collected from different regions of the Cape Province, and at different times ..... 226

Figure 103. Frequency histograms showing the percentage of lambs that are removed by predators before weaning as estimated from questionnaire surveys and field surveys based on necropsies carried out on lamb carcasses ..... 242

Figure 104. The findings of worldwide field necropsy surveys on lamb mortality summarised by geographical region . 245

Figure 105. The relationship between hyrax recruitment and the amount of rain falling during the gestation period .. 268

Figure 106. Annual plots of mortality and recruitment affecting the hyrax population for the four years of intensive field study ..... 270

Figure 107. Summer rainfall patterns in the Matobo Hills, Zimbabwe, and concordant change in the effort and success of black eagle breeding attempts monitored by Gargett (1990) ..... 274

Figure 108. Bounties paid out for the destruction of hyrax in the Cape Province between 1947 and 1955, and rainfall patterns over the same period ..... 274

Figure 109. Rainfall patterns recorded at Beaufort West and Stolshoek over the last century ..... 275

Figure 110. Schematic flow-diagram of the hyrax population model ..... 276

Figure 111. Changes in two versions of hyrax carrying capacity (per eagle territory) predicted by standard runs of the model ..... 279

Figure 112. A comparison of predicted change in hyrax density using two model versions for runs with the full complement of predation and for runs with eagles removed ..... 281

University of Pretoria etd – Davies, R A G (1994)



Page

Figure 113. Changes in winter phytomass, fresh growth and hyrax population density predicted by a standard run of the model with the full complement of predation ..... 285

Figure 114. Changes in the carrying capacity of a standard eagle territory for hyrax and concordant changes in hyrax population density predicted by a standard run of the model ..... 286

Figure 115. Changes in winter phytomass, fresh growth and hyrax population density predicted by a standard run of the model, but with hyrax conception rates modelled on preceding summer rainfall rather than P:K ratio ..... 287

Figure 116. Changes in hyrax population density predicted by a standard run of the model and by a run of the model where juvenile hyrax sex ratios were allowed to vary with rainfall ..... 288

Figure 117. Changes in hyrax population density predicted by a standard run of the model and by a run of the model where eagles were assumed to catch hyrax population classes in direct proportion to their availability. 289

Figure 118. Changes in winter phytomass, fresh growth and hyrax population density predicted by a run of the model with predation by black eagles removed ..... 290

Figure 119. Hyrax population change predicted by the model with and without predation by black eagles ..... 290

Figure 120. Changes in the carrying capacity of a standard eagle territory for hyrax and concordant changes in hyrax population density predicted by a run of the model with predation by black eagles removed ..... 291

Figure 121. Total number of hyrax dying, hyrax kill by eagles and potential hyrax kill by caracals as predicted by a standard run of the model ..... 291

Figure 122. Annual surplus of hyrax and potential hyrax kill by caracals as predicted by a standard run of the model 292

Figure 123. The demand for alternate (non-hyrax) prey by black eagles and caracals, as predicted by a standard run of the model ..... 292

Figure 124. Predicted changes in hyrax population density for different runs of the model with varying levels of predator impedance ..... 293

Figure 125. Predicted increment of average hyrax population density and population variability, and decrement of average winter phytomass, for increasing levels of predator impedance ..... 294

Figure 126. Predicted linear increment in hyrax surplus per eagle territory for increasing levels of predator impedance ..... 294

Figure 127. The predicted departure of hyrax population change in a standard run of the model when black eagles are impeded by 50% and when caracals are impeded by 50% ..... 295

Figure 128. Observations of hyrax population change in a standard eagle territory in the KRNP, in comparison with predictions of hyrax population change from two versions of the model for the same period ..... 296

Figure 129. Changes in winter phytomass, fresh growth and hyrax population density predicted by a standard run of the model using Stolshoek rainfall data ..... 297

Figure 130. Changes in winter phytomass, fresh growth and hyrax population density predicted by a standard run of the model using rainfall data from 32 sites in the Beaufort West District .. 298

Figure 131. Changes in winter phytomass, fresh growth and hyrax population density predicted by a standard run of the model using rainfall data for the Matobo Hills ..... 298

Figure 132. Predicted changes in hyrax population density for three variations of K_factor (the difference of P from K necessary to invoke maximal or minimal values of mortality and fecundity) in the model ..... 301

University of Pretoria etd – Davies, R A G (1994)

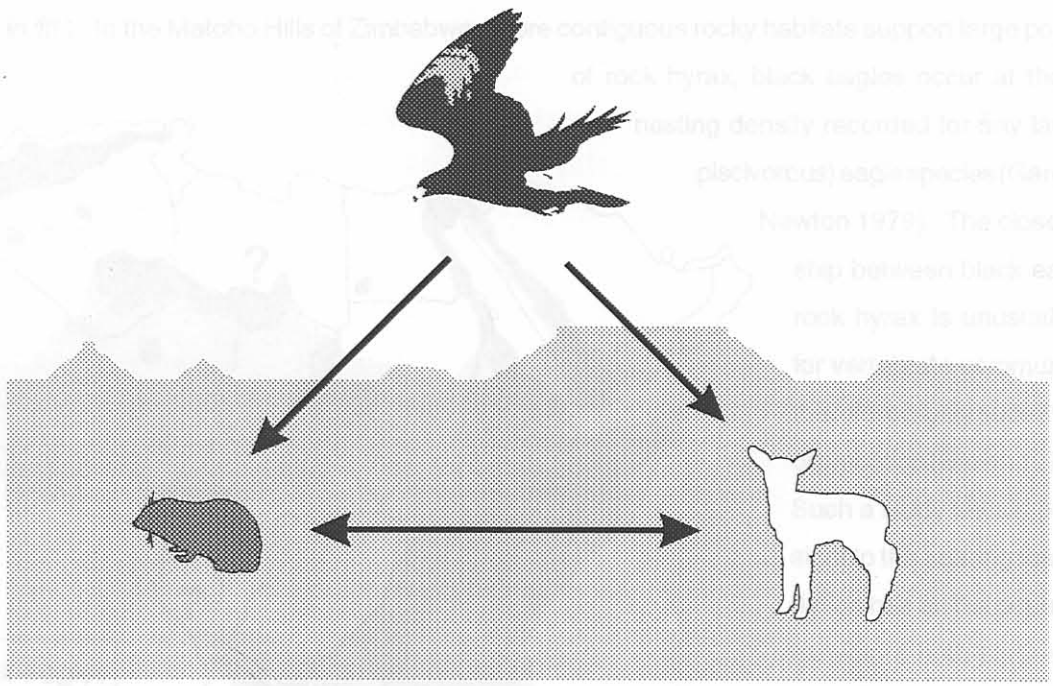
# *GENERAL INTRODUCTION*

*"'Whether or not vertebrate predators regulate their prey?' is currently debated among animal ecologists, as this question is important to issues of pest control, wildlife ecology and conservation of rare species."*

(Korpimäki 1993)

*"The preference for rock hyrax almost to the exclusion of other prey makes Verreaux's Eagle a very good subject for a close study of the predator-prey relationship. ..... It should be possible to ascertain the total range of a pair, the approximate number of hyrax in that range, and the effect of the eagles upon the hyrax population, with a degree of accuracy which would be elusive with most species of eagles."*

(Leslie Brown 1970)



*"The question of predation by various species of eagles on livestock, especially sheep, has been vigorously debated on several continents and has been a major concern in the management of both kinds of populations. An effective understanding of this often complex problem cannot be achieved in an atmosphere of bitterness and acrimony, and it is therefore essential that accurate information from research studies by disinterested parties be acquired wherever possible."*

(Murphy 1976)

University of Pretoria etd – Davies, R A G (1994)



CHAPTER 1

# *INTRODUCTION AND GENERAL APPROACH*

The mountains and koppies (inselbergs) of Africa can be inhospitable places to live. Small mammals inhabiting these areas are often exposed to extreme climatic variation and a wide array of predators. Furthermore, burrowing to escape these adversaries is not usually an option in the rugged, rocky terrain. Rock hyrax or 'dassies' (genus *Procavia* and *Heterohyrax*) solve these problems by taking refuge in rock crevices and interstices. They are well adapted to this lifestyle (Sale 1970a), and are often the most abundant small to medium-sized, mammalian herbivore encountered in the rocky parts of sub-Saharan Africa. The successful exploitation of these habitats by hyrax since perhaps the Oligocene (Sale 1970a), has permitted and possibly encouraged the evolution of a large avian predator, the black or 'Verreaux's' eagle *Aquila verreauxii*, which is reportedly highly prey-specific to rock hyrax (Brown 1952, 1970; Vernon 1965; Gargett 1977, 1990; Steyn 1982; Tarboton & Allan 1984). The current distribution of black eagles coincides with that of rock hyrax and mountains in most parts of Africa, but they are inexplicably absent from the Sahel (Fig. 1; Thiollay *in litt.*). In the Matobo Hills of Zimbabwe where contiguous rocky habitats support large populations of rock hyrax, black eagles occur at the highest nesting density recorded for any large (non-piscivorous) eagle species (Gargett 1975; Newton 1979). The close relationship between black eagles and rock hyrax is unusually simple for vertebrate communities and therefore highly suited to a study of predation (Brown 1970: p112). Such a study should provide insight to the bearing that this predation has on the population dynamics of both parties, as well as an indication of its evolutionary consequences in terms of form and behaviour. Yet, although both predator and prey have received considerable scientific attention separately (see Chapters 4 & 6 for more detail), their relationship to one another has not been looked at in any detail.

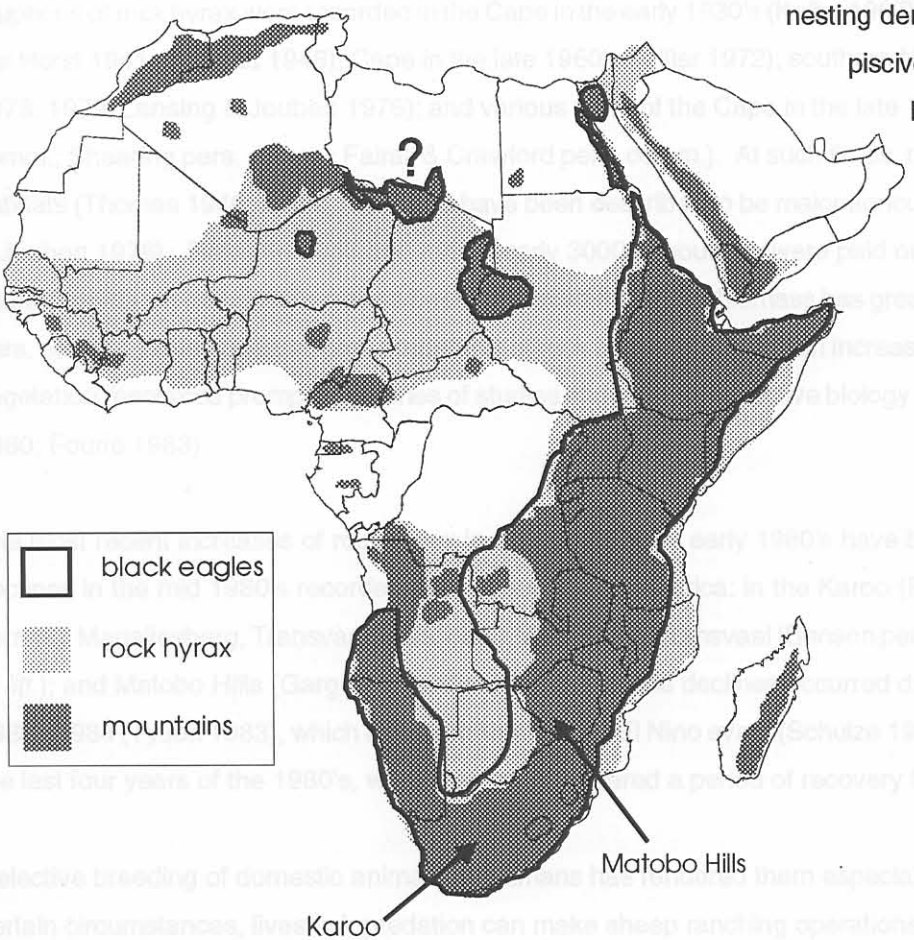



Figure 1. Distribution patterns of mountains (from Anon 1970), rock hyrax (after Bothma 1971; Kingdon 1971; Fourie 1983; Skinner & Smithers 1990) and black eagles (after Snow 1978 & Thiollay *in litt.*) in Africa.

University of Pretoria etd – Davies, R A G (1994)



In the Karoo of South Africa, relationships between rock hyrax (*Procavia capensis*) and their predators take on added significance because both are reputed to interfere with the farming of small livestock. Karoo veld or vegetation spans most of the interior of the Cape Province and extends into southern Namibia. It is maintained as a dwarf shrubland by the influence of a semi-arid climate. Annual rainfall is less than 250mm in most karoo regions (Cowling 1986). The extent of karoo veld in South Africa is 427000km$^2$, representing 23% of the nation's land area and 41% of the natural pasture (Roux, Vorster, Zeeman & Wentzel 1981; Vorster & Roux 1983). Since the advent of the European settlers, the principal land-use in the Karoo has been the open-range farming of small domestic livestock for the production of meat, wool and mohair. The Karoo currently supports a population of nearly ten million small livestock. Numbers have been reduced by 60% since the wool boom in the 1930's (Roux *et al.* 1981), but overgrazing continues to cause degradation of the vegetation resource (see Chapter 2). Livestock in the Karoo are not managed intensively and are at risk to any large predators in the region, particularly in the inaccessible, rocky areas. Koppies and flat-topped mountains comprise 15% of the eroded Karoo landscape (Roux *et al.*1981). Resistant 'caps' of sandstone or dolerite protect the underlying cones of soft mudstones, and provide ideal conditions for rock hyrax and their predators.

Normally hyrax graze and browse only in the rockiest habitats where sheep seldom venture, and competition for available forage on Namibian farmland has been described as negligible (Lensing 1979, 1982). However, major irruptions of rock hyrax were recorded in the Cape in the early 1930's (Kolbe 1967); Cape Midlands in the 1940's (van der Horst 1941; Thomas 1946); Cape in the late 1960's (Millar 1972); southern Namibia in the late 1960's (Lensing 1978, 1979; Lensing & Joubert 1976); and various parts of the Cape in the late 1970's / early 1980's (Wilmot pers. comm.; Shearing pers. comm.; Fairall & Crawford pers. comm.). At such times, rock hyrax may colonise non-rocky habitats (Thomas 1946; Kolbe 1967) and have been described to be major agricultural pests (Hanse 1962; Lensing & Joubert 1976). Between 1947 and 1957 nearly 300000 bounties were paid out for the destruction of rock hyrax (Norton *in litt.*). In certain areas it has been estimated that hyrax biomass has greatly exceeded that of sheep (Fairall pers. comm.). This observed high propensity of rock hyrax for population increase, and the threat that this posed to vegetation resources prompted a series of studies on hyrax reproductive biology in South Africa (Millar 1971; Steyn 1980; Fourie 1983).

The most recent increases of rock hyrax in the late 1970's / early 1980's have been followed by major population declines in the mid 1980's recorded throughout southern Africa: in the Karoo (Fairall 1991, *in litt*; Swiegers pers. comm;); Magaliesberg, Transvaal (pers. obs.); Waterberg, Transvaal (Benson pers. comm.); Drakensberg (Bowland *in litt.*); and Matobo Hills (Gargett & Banfield *in litt.*). These declines occurred during or after the 'great drought' of 1983 - 1984 (Tyson 1983), which has been linked to an El Nino event (Schulze 1983). The present field study spans the last four years of the 1980's, which can be considered a period of recovery for karoo biota.

Selective breeding of domestic animals by humans has rendered them especially vulnerable to predators. Under certain circumstances, livestock predation can make sheep ranching operations untenable (e.g. O'Gara, Brawley, Munoz & Henne 1983). Many karoo farmers believe that black eagles kill small livestock, especially juveniles. This belief is based mostly on hearsay accounts and traditional notions (pers. obs.). Brown (1975) argued that diet studies have largely exonerated the bird. But more recent investigations in the Cape Province have confirmed that domestic

University of Pretoria etd – Davies, R A G (1994)



lamb remains are indeed found in varying amounts at black eagle nest sites (Boshoff, Palmer, Avery, Davies & Jarvis 1991). However, nest-based diet studies do not give a good indication of the problem (Matchett & O'Gara 1987), and the real extent of livestock predation by black eagles in the Karoo has not been properly researched.

Despite this, persecution of eagles by farmers in the Karoo has been very intense. Five thousand bounties were paid out for the destruction of eagles in the Cape Province between 1930 and 1955 (Boshoff & Vernon 1980). This represents a kill rate of three eagles 10000km$^{-2}$ y$^{-1}$, and may be underestimated. In the 1960's farmers in the Philipstown district claimed a kill rate of 20 eagles (mostly martial eagles *Polemaetos bellicosus*) 10000km$^{-2}$ y$^{-1}$; while farmers in the Laingsburg district claimed a kill rate of 166 eagles (mostly black eagles) 10000km$^{-2}$ y$^{-1}$ (Siegfried 1963a). The wedge-tailed eagle *Aquila audax* in Australia was once described as the most heavily persecuted large raptor (Brown, L.H. 1976: p195). Over a 38y period in western Australia, approximately 18 wedge-tailed eagles were killed 10000km$^{-2}$ y$^{-1}$, and it was thought that this may have caused population declines in unstable areas (Ridpath & Brooker 1986). Large eagles are long-lived and have a relatively low reproductive output, so it is very likely that such persecution by humans has contributed to the world-wide decline in these birds (Brown 1976; Newton 1979). The extremely high kill rate claimed for black eagles in Laingsburg is nearly twice the expected annual production of juveniles for the population in that district. Such areas would have acted as a sink for the Cape eagle population, and it seems likely that these levels of persecution would have caused population declines in large areas of the Cape and the Karoo in the past.

Naturalists have argued that the destruction of predators and the irruptions of rock hyrax are linked. Rock hyrax are natural prey for a variety of predators that have been killed in large numbers in control operations in the Karoo, especially caracals *Felis caracal* and black eagles. Caracals can be described as generalist predators: they take a wide variety of prey and are sufficiently powerful to pose a serious threat to adult sheep and goats (Pringle & Pringle 1980; Moolman 1986a, 1986b). A total of 26220 caracals were killed in the Cape Province between 1931 and 1943 (Moolman 1986a). Control operations continue in earnest but caracals remain the major 'problem animal' in this province (Stuart 1981). In the eastern Karoo, where black eagles may be nest-site limited, they are considered to be the major hyrax predator and their relationship to this prey has been fairly extensively researched and modelled mathematically (Grobler 1981; Fourie 1983; Swart, Perrin, Hearne & Fourie 1986). It is believed by some that the destruction of black eagles, caracals and other predators has led directly to the population irruptions of the fecund rock hyrax and consequent damage to the vegetation resources (Thomas 1946; Kolbe 1967; Rubidge in Kolbe 1983). The coincidence of major hyrax irruptions with the completion of jackal-proof fencing and the onset of effective predator control in both the Karoo in the early 1930's (Pringle & Pringle 1979; Rubidge in Kolbe 1983) and in Namibia in the late 1960's (Lensing & Joubert 1976) provides circumstantial evidence in favour of this hypothesis.

I became personally interested in this topic when I visited the farm Montana near Victoria West in the Karoo in 1984. Predator control had been very intense on this farm, with as many as 78 caracals killed in the previous six years. The farm appeared to be over-run with rock hyrax which were to be seen in large numbers, well away from rocky habitats and apparently very vulnerable. The farmer showed me thousands of hyrax skins from animals that he had shot but this apparently had not been sufficient to prevent a major irruption. By August 1984 the grazing resources had deteriorated to such an extent that the farmer was forced to move his livestock to a farm near Britstown. Subsequently

University of Pretoria etd – Davies, R A G (1994)



most of the hyrax disappeared (in synchrony with population declines elsewhere) and the farmer brought his livestock back to Montana six months later, after the veld had received rainfall.

A link between this irruption of rock hyrax and the intensive predator control campaign seemed obvious at the time. But traditional notions about 'the balance of nature' have been increasingly displaced by the observation of unpredictable or chaotic ecosystem behaviour (May 1989), and the long-lasting debate about whether predators actually 'control' their prey or not is far from resolved (see review in Chapter 12). Many ecologists still follow Errington's (1946, 1963) belief that predators merely remove a doomed surplus of their prey, and Siegfried (1963a) stated "In many cases, the value of eagles, as a means of combating and controlling the dassie (hyrax) plague has been accorded exaggerated importance". I felt that this issue would be worthy of detailed investigation. The relationships between rock hyrax, black eagles and domestic livestock in the Karoo are summarised in Figure 2:

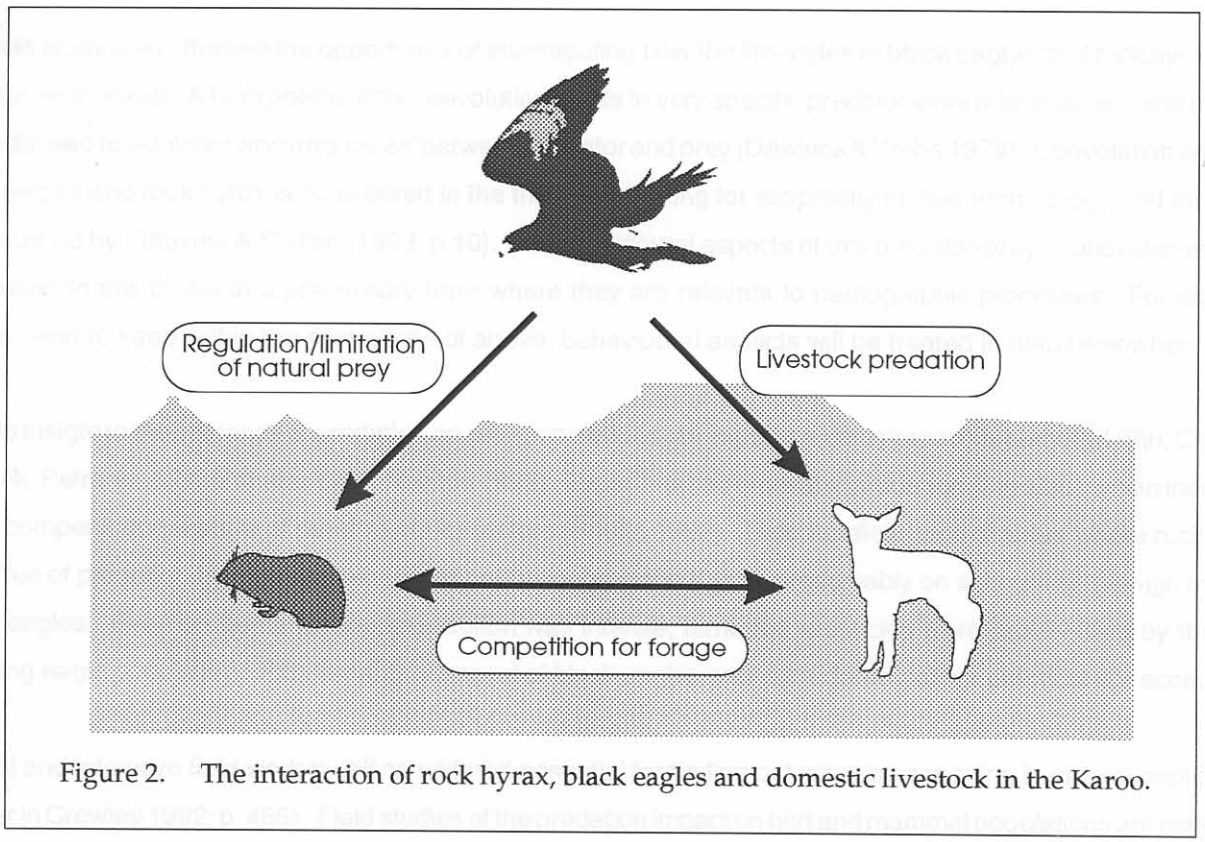



Figure 2. The interaction of rock hyrax, black eagles and domestic livestock in the Karoo.

By seeking an understanding of predator-prey relationships within this system, I attempt to resolve two principal controversies in this thesis:

1. **do predators such as black eagles limit or regulate rock hyrax populations in the Karoo?**
   (and, can it be inferred that hyrax irruptions were caused by predator control?)

2. **do eagles kill domestic livestock in the Karoo?**
   (if so, to what extent does this occur, under what circumstances, and how can it be avoided or minimised)

University of Pretoria etd – Davies, R A G (1994)


This study of a rather unique vertebrate predator-prey system was largely intended as an academic contribution in the field of population biology. Even if predation proved unimportant as a factor affecting hyrax population change, it was hoped that this study would still shed some light on other factors responsible for the obvious increase and decline phases that so characterise rock hyrax populations in the Karoo. By necessity, much of the attention in this thesis revolves around rock hyrax demographic processes. The entire scope of this thesis however, relates to the usefulness of this research in clarifying the ecological role of a controversial and potentially vulnerable predator on farmland, and I have endeavoured to address both the harmful and the beneficial influences of black eagles as thoroughly as possible. It is sincerely hoped that the findings herein will benefit farmers and conservationists alike, and help prevent the development of rifts between these parties which have plagued the contentious issue of livestock predation by large eagles in the past (Murphy 1976). Although the system under study is highly specific, the principles gained on relationships between eagles and their prey may find wider application.

The field study also afforded the opportunity of investigating how the life-styles of black eagles and rock hyrax have become inter-linked. A high potential for coevolution exists in very specific predator-prey relationships, and this can allegedly lead to 'evolutionary arms races' between predator and prey (Dawkins & Krebs 1979). Coevolution between black eagles and rock hyrax is considered in the thesis by looking for reciprocity in their morphology and ethology, as described by Futuyma & Slatkin (1983: p.10). But behavioural aspects of this predator-prey relationship are only introduced to this thesis in a preliminary form where they are relevant to demographic processes. For logistical reasons and to keep within the scope set out above, behavioural aspects will be treated in detail elsewhere.

To gain insight to the influence of predation on prey populations, an experimental approach is favoured (Sih, Crowley, McPeek, Petranka & Strohmeier 1985; Newton 1992). Experimental removal of predation may also give an indication of the compensatory nature of other mortality factors (Boutin 1992). Unfortunately control areas where rock hyrax were free of predation by black eagles, could not be found in the Karoo, presumably on account of the high mobility of the eagles. Even on farms where persecution was intense, territorial vacancies were rapidly filled by the non-breeding eagle population. Experimental removal of black eagles was considered neither practical nor acceptable.

Careful and intensive field work is still considered essential for finding out what is happening in natural populations (Endler in Crawley 1992: p. 486). Field studies of the predation impact on bird and mammal populations are especially needed (Sinclair 1989). So the approach adopted in this study was to intensively describe the black eagle - rock hyrax system over a five year field study under natural conditions in a conserved area of the Karoo where predators had not been persecuted for at least seven years (livestock predation by black eagles was researched concurrently on neighbouring farmland). Some previous monitoring of hyrax and caracals in the conserved area (Fairall 1991, *in litt.*; Palmer & Fairall 1988) provided background for the present study. Certain key elements were recognised as important components in the natural system:

1. refuge-dependent rock hyrax
2. a popular alternate prey species, Smith's red rock rabbit *Pronolagus rupestris*
3. permanent and patchy distribution of the refuge resource

which determines a fixed extent of safely-accessible vegetation for rock hyrax

University of Pretoria etd – Davies, R A G (1994)



4. periodic enrichment of this lower trophic level by seasonal and somewhat cyclical rainfall interspersed by severe drought
5. predation by 'specialist' black eagles
6. predation by 'generalist' caracals

It was felt that inferences on the demographic influence of black eagles on rock hyrax could not be drawn unless all interacting elements within the system were researched. So data were sought on all key elements to provide a comprehensive understanding, and to construct 'as good a model as possible' of the system. This population model of rock hyrax is run using climatic data for the last century to effectively extrapolate the period of investigation into the long term. Those factors which most influence rock hyrax population change are examined empirically during the short-term field study and theoretically using the long-term predictions of the model. Experimental removal or impedance of predators is simulated and examined by use of the model, and the resulting cost in terms of damage to grazing resources by hyrax surpluses is predicted. This approach of using models to conduct factor analyses and to test hypotheses generated from empirical field studies has been endorsed for the study of predator-prey interactions (Hansson 1988a).

The first half of this thesis provides the necessary background information on the study environment (Chapter 2), the refuge resource (Chapter 3), the prey base (Chapters 4 & 5), and the predator guild (Chapters 6 & 7). This involves much description and general biology. Field research on caracals was not as successful as hoped, but extensive reference could be made to the findings of other researchers in Chapter 7. The second half of the thesis deals with the interaction of predator and prey (beginning with some treatment of the impact of caracals on hyrax in Chapter 7). Feeding habits of black eagles are treated in three separate chapters: prey capture rate (Chapter 8); the selection of prey species (Chapter 9); and the selection of rock hyrax population classes (Chapter 10). Livestock predation by black eagles is addressed in Chapter 11. On account of the difficulty in finding any evidence of stock predation by black eagles, this chapter includes a worldwide literature review of livestock predation by eagles. The information provided in previous chapters is then collated and used in the model to assess the demographic influence of black eagle predation on rock hyrax in Chapter 12. Reciprocal behavioural and morphological traits of black eagles and rock hyrax are considered in the synthesis which includes an appraisal of this predator-prey system in comparison to others, and a costs/benefits analysis of black eagles on karoo farmland.

NOTE

the addresses of all persons cited 'pers. comm.' or *'in litt.'* in this thesis may be found in Appendix 11 on the last page.

University of Pretoria etd – Davies, R A G (1994)

# *ENVIRONMENT AND THE REFUGE RESOURCE*



University of Pretoria etd – Davies, R A G (1994)



CHAPTER 2

# *STUDY ENVIRONMENT*

*Karoo*

To the north and south of the equatorial belt, Africa has always been a drought-ridden continent (Kingdon 1990). The south-west regions of Africa, encompassing Namibia, half of Botswana and the Cape Province of South Africa, are especially starved of moisture because the Benguela current, which runs north along the west coast drawing water from Antarctica and from the ocean depths, is too cold for extensive evaporation. Cyclonic weather fronts from Antarctica bombard the south-west tip of Africa in winter with expansion of the circum-polar vortex but most of this moisture is shed orographically as the fronts hit the Cape Fold Mountains, and this mediterranean climate has given rise to the richest and smallest floristic kingdom in the world, the Fynbos (Hilton-Taylor & Le Roux 1989). Likewise, moist air emanating from the warm Indian ocean in the east is prevented from reaching the interior by the high peaks of the Drakensberg escarpment. Only rarely do the tropical, anticyclonic weather systems push far enough south to bring thunderstorms to the arid south-west in summer. This dry corner of Africa, the Namib-Karoo, has become a centre of endemism for many arid-adapted plants and animals (Kingdon 1990).

The name 'Karoo' derives from 'Karu', a Khoisan word translated as 'the place of great dryness'. Traditionally, Karoo referred to the arid interior of the Cape Province, an area of some 427000km$^2$ characterised by its eroded landscape of koppies (inselbergs) and flat-topped mountains and by its thin covering of small shrubs. Ecologists now use the word karoo to describe this characteristic dwarf shrubland as a veld (vegetation) type which extends to the west coast of the Cape (Namaqualand) and northward, encompassing most of southern Namibia, but narrowing as it becomes sandwiched by the truly arid Namib desert along the west and the moister arid savannah along the east, to disappear near the coast in southern Angola (Fig. 3). The total extent of karoo veld in southern Africa probably exceeds 700000km$^2$. Most areas supporting karoo veld receive less than 250mm rain per annum (Cowling 1986), and can be described as semi-arid or arid. However, annual rainfall varies along a gradient from less than 100mm in the western extremes to over 500mm in the eastern limits (Venter, Mocke & de Jager 1986). While the distinction between the Karoo and the Namib desert is fairly accepted, the borders between karoo veld and the moister arid savannah in the southern Kalahari, and the moister grasslands in the southern Orange Free State are changeable and still under debate (Acocks 1953; Werger 1986; Hoffman & Cowling 1987, 1990a). Classification of these regions as arid or semi-arid deserts is also dependent on variation in solar radiation and soil types which affect loss and retention of water.

Karoo veld covers 35% of South Africa but receives only 10% of the nation's rainfall. This area suffers drought (as defined as <60% mean annual rainfall) for 30-50% of the time, and in some areas droughts may last longer than three years (Roux & Opperman 1986). Aridity is probably the major factor which enables dwarf shrubs to dominate the grass component in karoo flora, but weak soils, herbivory and the absence of fires may also be involved. Dwarf shrubs or chamaephytes in karoo veld are either non-succulent (especially *Asteraceae* e.g.. *Pentzia incana*, *Eriocephalus ericoides*) or succulent (especially *Mesembryanthemaceae* e.g.. *Ruschia* spp.). These shrubs are usually thinly spread and rarely project more than 30cm above or below ground level (Hoffman & Cowling 1987). Although

University of Pretoria etd – Davies, R A G (1994)



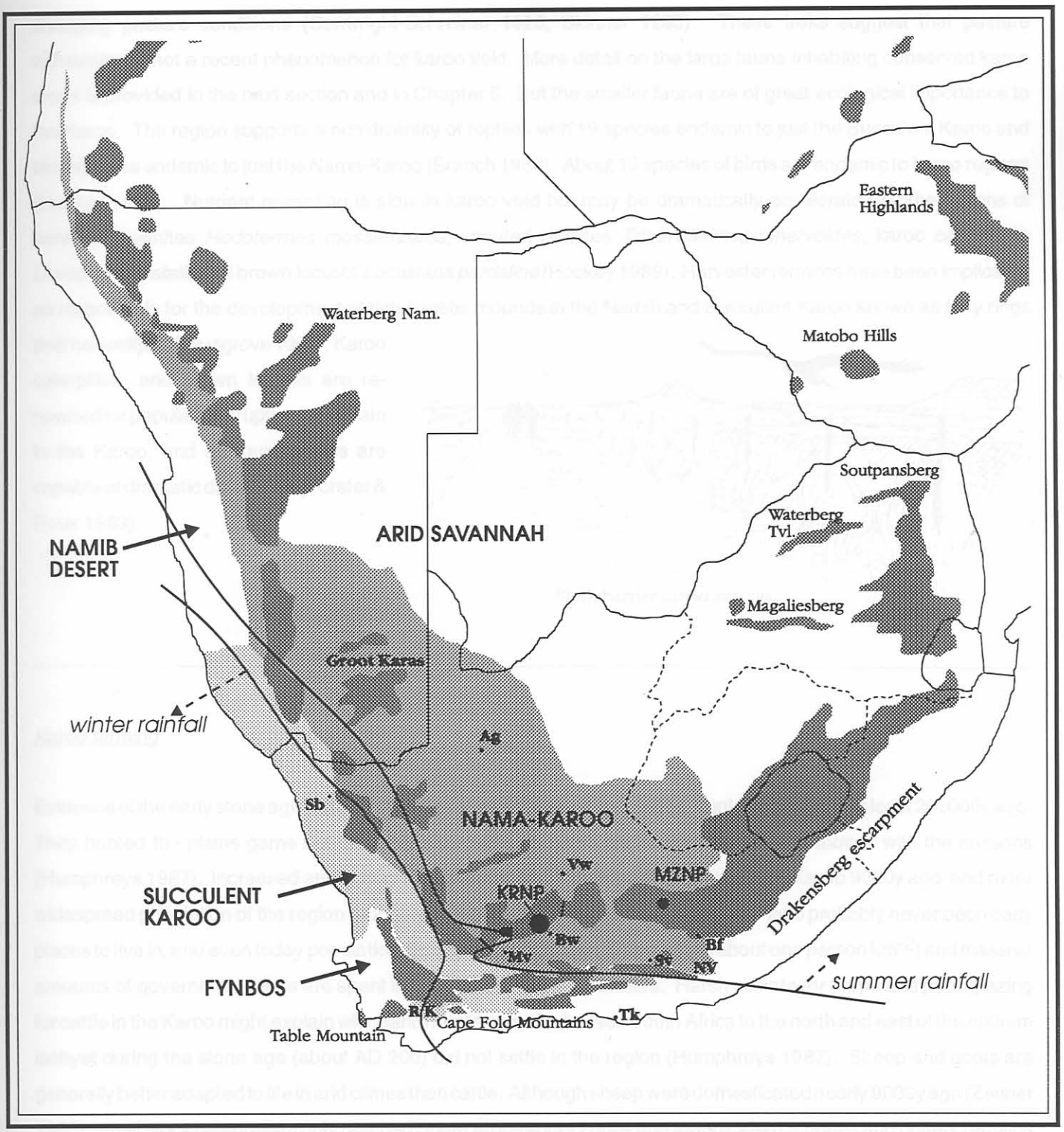
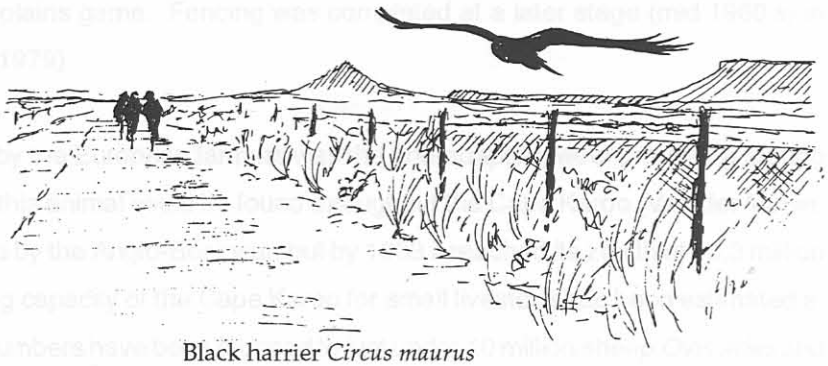



**Figure 3.** Distribution of mountains (dark grey), Nama-Karoo (grey) and Succulent Karoo (pale grey) in southern Africa (from Anon 1970; Cowling 1986; Kingdon 1990; and Lovegrove 1993). Summer rainfall regions are separated from winter rainfall regions by continuous lines (after Werger 1986). The belt in between these receives rain at any time of the year. From hashed lines representing provincial boundaries within South Africa (as at 1993), it is evident that karoo veld occupies most of the Cape Province and some of the southern Orange Free State. Mountain ranges referred to in this thesis are named in full. Place names are abbreviated. KEY: Sb Springbok (Namaqualand); Ag Augrabies Falls National Park; Vw Victoria West; Bw Beaufort West; Mv Merweville; Sv Steytlerville; Bf Bedford; Tk Tsitsikama; NV Noorsveld; RK Robertson Karoo; MZNP Mountain Zebra National Park; KRNP Karoo National Park. The KRNP lies in the Nuweveldberg which links with the Roggeveldberg to the west and with the Sneeu/Winterberg to the east. These contiguous ranges are separated by dark lines. The Sneeu/Winterberg link to the southern Drakensberg to the east of the MZNP. A dark rectangle denotes the study area of Boshoff & Palmer (1988) 80km west of the KRNP (see text).

University of Pretoria etd – Davies, R A G (1994)



changing pasture conditions (Conwright-Schreiner 1925; Skinner 1993). These treks suggest that pasture exhaustion is not a recent phenomenon for karoo veld. More detail on the large fauna inhabiting conserved karoo areas is provided in the next section and in Chapter 5. But the smaller fauna are of great ecological importance to the Karoo. The region supports a rich diversity of reptiles with 19 species endemic to just the Succulent Karoo and nine species endemic to just the Nama-Karoo (Branch 1988). About 19 species of birds are endemic to karoo regions (Huntley 1984). Nutrient re-cycling is slow in karoo veld but may be dramatically accelerated by the actions of harvester termites *Hodotermes mossambicus*, snouted termites *Trinervitermes trinervoides*, karoo caterpillars *Loxostega frustalis* and brown locusts *Locustana pardaline* (Hockey 1988). Harvester termites have been implicated as responsible for the development of rich floristic mounds in the Namib and Succulent Karoo known as fairy rings and 'heuweltjies' (Lovegrove 1993). Karoo caterpillars and brown locusts are renowned for population irruptions after rain in the Karoo, and all four species are capable of dramatic defoliation (Vorster & Roux 1983).



Black harrier *Circus maurus*

---

*Karoo farming*

Evidence of the early stone age indicates that Karoo regions were peopled by 'hunter-gatherers' at least 200000y ago. They hunted the plains game but probably also relied on some staple food plants, and moved with the seasons (Humphreys 1987). Increased aridity may have caused some depopulation of the Cape Karoo 9000y ago, and more widespread population of the region probably only began 4000y ago. Karoo regions have probably never been easy places to live in, and even today population density in this part of the Cape is low (about one person $km^{-2}$) and massive amounts of government funds are spent in drought aid to karoo farmers. Harsh climate for crops and poor grazing for cattle in the Karoo might explain why Bantu farmers who colonised South Africa to the north and east of the 400mm isohyet during the stone age (about AD 200) did not settle in the region (Humphreys 1987). Sheep and goats are generally better adapted to life in arid climes than cattle. Although sheep were domesticated nearly 9000y ago (Zeuner 1963), small stock pastoralism only reached South Africa about 2000y ago as indicated by bones and pottery remains found down the west coast into the south-west Cape (Humphreys 1987). Evidence of historic (<2000y ago) over-grazing has been found in one isolated locality (Sampson 1985), but extensive (sedentary) herding of small stock on karoo veld probably only began with the movements of the Europeans and Khoi-khoi from the south-west Cape in the late 1700's. Undoubtedly the single most important factor which enabled this exploitation of karoo veld was the ability of these farmers to tap into the extensive underground water systems which lie in sandstone joints and along dolerite dykes not far below most of the karoo surface, and thus to supply drinking water to their domestic animals in otherwise uninhabitable areas. Most boreholes in the Karoo are driven by regular winds and require only maintenance. Their water supply may vary from 1 $lsec^{-1}$ in the arid west to 4 $lsec^{-1}$ in the moister eastern regions (Hodgson 1986).

University of Pretoria etd – Davies, R A G (1994)



The plains game that roamed the Karoo were hunted by the European immigrants on an unprecedented scale for sport and to clear the way for the livestock. Quaggas were initially very numerous (Harris 1840), and probably largely endemic to karoo regions. But the hunting led to the total extermination of quaggas and also bluebuck *Hippotragus leucophaeus* (south of the Cape Fold Mountains), and devastation of most other game populations. Today, only springbok (96% farms) and to a lesser extent blesbok *Damaliscus dorcas phillipsi* (22% farms) are seen regularly on karoo farms, and these usually in small numbers (Jooste 1983). The larger predators were also killed off. Black-back jackals *Canis mesomelas* survived in most karoo areas, and in a massive campaign to control this predator and to enable more intensive livestock management, the entire Cape Karoo was fenced off into paddocks by the 1920's (Pringle & Pringle 1979), and this has been maintained at enormous expense (Siegfried *in litt.*). These fences prevented the movements of any surviving plains game. Fencing was completed at a later stage (mid 1960's) in Namibia (Lensing & Joubert 1976; Lensing 1979).

The breed of small livestock most favoured by the European farmers was the arid-adapted, wool-producing Merino sheep, and by 1820 substantial numbers of this animal could be found throughout the Cape Karoo (Van der Merwe 1938). Growth of the karoo flock was slowed by the Anglo-Boer war, but by 1933 it reached its zenith of 40,3 million woolled sheep. The long-term 'safe' carrying capacity of the Cape Karoo for small livestock has been estimated at 7 - 7,5m animals, and since the wool boom numbers have been reduced to just under 10 million sheep *Ovis aries* and goats *Capra hircus* (Roux *et al.* 1981). The Cape Karoo flock now comprises 4745363 woolled sheep, 3449110 mutton sheep, 959803 Angora goats and 354996 Boer goats (Department of Agriculture, Middelberg, *in litt.*). Most of these livestock are maintained under open-range conditions and are heavily reliant on the farmer for protection from disease and predators, for water and for feed during drought. Goats and meat-producing sheep are favoured in arid regions or in difficult terrain (thickets and rocky areas). Only 8% of the Karoo (the endangered riverine habitat) has been suitable for cultivation (Roux *et al.* 1981). Karoo livestock provide 36% of the wool, 48% of the mutton, 60% of the mohair and 60% of the goat meat produced in South Africa (one of the six largest wool-producing nations in the world). Karoo veld, on which the livestock rely, is thus an important national resource in South Africa. Through growth of the human population and a tradition of subdividing land between sons, farms in the Cape Karoo have become progressively smaller. There are now 8972 farms in the Cape Karoo, owned by 6200 farmers (Department of Agriculture, Middelberg, *in litt.*). The average karoo farmer thus manages about 4700ha and just over 1500 small livestock. These produce about 820 lambs p.a. during one or two distinct lambing seasons which are geared to maximise production (Roux *et al.* 1981). In Beaufort West most lambs (65%) are born in March. It has been calculated that karoo farms need to support 1200 small livestock to be economically viable, and many fall well below this target.

The once wide variety of nomadic herbivores has been replaced by intensively-stocked monocultures of small livestock with specialist feeding habits. Nearly 200y of this treatment has had a devastating effect on karoo soils and vegetation in most areas. Prolonged heavy grazing is considered to suppress shoot/root formation and flowering in karoo flora (Cowling 1986) which leads to depletion and thinning out of the vegetation, particularly those components which sheep find palatable (Vorster, Botha & Hobson 1983). Intense damage from grazing and trampling is found around water points on which sheep are highly dependent in the Karoo (Davies & Skinner 1986). Thinning of the already sparse vegetation layer has greatly accelerated rates of soil erosion (mainly sheet, gulley, splash and wind erosion). Experimental continuous heavy grazing for 25y caused depletion of the top 15cm of the orthic A horizon

University of Pretoria etd – Davies, R A G (1994)



in the top soil (Roux & Opperman 1986). Just removal of the top 1-5mm by wind erosion can kill seedlings (Roux 1960). It is estimated that rivers carry 32 million $m^3$ of sediment from the Karoo each year (Midgley undated). Soil erosion has been described as the biggest environmental and agricultural problem in South Africa, and although 70% of Karoo farms have been planned to reduce erosion only a small minority of these farms implement the recommendations (Roux & Opperman 1986).

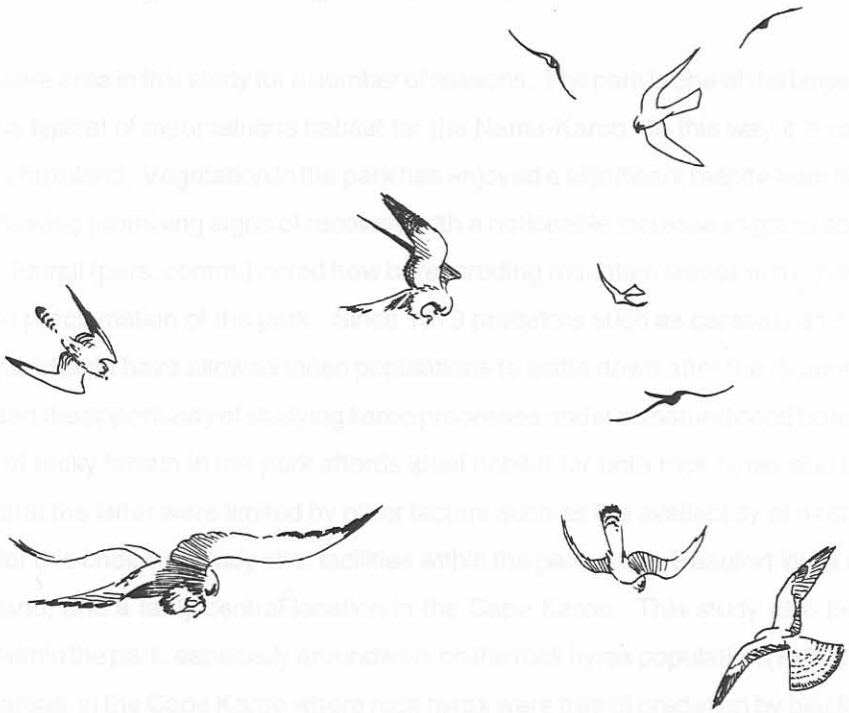
Where the dry compact B soil horizon is exposed by erosion, the more hardy brack grasses and less palatable shrubs take hold. Roux & Vorster (1983) contend that most of the Cape Karoo is in a third phase of desertification where unpalatable species are revegetating areas cleared of the palatable plants in a process of succession. Non-succulent chamaephytes are better suited for colonising bare ground and surviving droughts than grasses (unfortunately they afford less protection to the topsoil). Acocks (1953) was the first to document and predict the replacement of sweet grassveld by karoo shrubs in the eastern regions. He predicted that karoo veld was spreading eastward at a rate of 2-3km per annum and that it would encompass most of the Orange Free State by 2050. Hoffman & Cowling (1990a) have used historical photographs and vegetation analyses to largely refute these predictions. These authors (1987) argue that karoo shrubs appear not from a succession process but rather through 'exadapation' to drought conditions, and that the southern Orange Free State and the eastern Cape form a highly dynamic interface between grassveld and karoo veld. However these same authors have found positive evidence of desertification in the lower Sundays River Valley (Noorsveld) where areas of subtropical thicket are being ousted by karoo shrubs (Hoffman & Cowling 1990b), and there can be little doubt that heavy grazing has had a major influence on the vegetation within karoo regions. Besides soil planning, management measures taken to curb this degradation have been rotational grazing, stock reduction and diversification of stock with other livestock breeds and with game (Vorster *et al.* 1983; Davies 1985). Although conditions are much improved since the wool boom, vegetation changes in the Karoo are now very difficult or even impossible to reverse.

Human activities have led to a reduction in the quality of the vegetation and in the diversity of animals living in karoo regions. Besides destruction of the plains game and potential predators of livestock (details of the bounty system are provided in Chapter 11), farmers have also persecuted aardvarks *Orycteropus afer* for their habit of digging holes under jackal-proof fences and allegedly allowing predators access to flocks. Predator control operations have involved placing gin traps in such holes under fences and innumerable bat-eared foxes *Otocyon megalotis*, aardwolves *Proteles cristatus* and other potentially important insectivores have been killed in this way. Many farmers still place gin traps and strychnine bait in and around sheep carcasses to kill potential predators, but it has been estimated that these indiscriminate methods may kill 100 non-target animals for every jackal or caracal (Brown 1988a). Strychnine is still widely available to karoo farmers and it is estimated that only 15% is sold legitimately. Use of poison is almost certainly responsible for the disappearance of large scavenging raptors such as Cape vultures *Gyps coprotheres*, lappet-faced vultures *Torgos tracheliotus*, bateleurs *Terathopius ecaudatus* and most tawny eagles *Aquila rapax* from the Cape Karoo (Allan 1989), and from parts of Namibia (Brown 1988a, 1991). Another poison which has been used extensively in karoo regions (to control outbreaks of brown locusts *Locustana pardaline*) is benzene hexachloride (BHC). Vast quantities of this chemical were used in control operations in 1985/1986 costing approximately R48 million (Hockey 1988). Extremely high levels of BHC contamination were subsequently recorded in many insectivores (Erasmus pers. comm.). The net result of these destructive human activities in karoo regions

University of Pretoria etd – Davies, R A G (1994)



has been the degradation and simplification of a once highly dynamic, diverse and somewhat vulnerable ecosystem. More simple ecosystems tend to be less stable (Simpson 1949). Removal or impedance of important components within the karoo system has been implicated in the aggravated irruptions of varied pest species which appear to be manifestations of this instability. Termite problems appeared to be aggravated on the farm Montana near Victoria West where heavy grazing and destruction of natural predators had occurred (pers. obs.). Destruction of vegetation resources by major outbreaks of karoo caterpillars *Loxostege frustalis*, has been linked to overgrazing and the spread of non-succulent chamaephytes (host plants, see Möhr 1982), and a reduction in natural predators may explain recent increase in the frequency of locust outbreaks (Hockey 1988). It is important that irruptions of rock hyrax should be viewed in this holistic perspective of change in karoo regions.



Lesser kestrels *Falco naumanni* catching brown locusts *Locustana pardaline* near Beaufort West (November 1989)

---

*Karoo National Park*

Despite the changes which are threatening the rich diversity of karoo biota only 1,2% of the Succulent Karoo and only 0,5% of the Nama-Karoo are currently protected within conserved areas (Hilton-Taylor & Le Roux 1989). Following a campaign by the South African Nature Foundation, the Karoo National Park (KRNP) was proclaimed in 1979 to protect an area of the Nama-Karoo. The park actually conserves a major buttress of the Nuweveld Mountains (Figs. 3 & 4) overlooking Beaufort West (32°21'S; 22°35'E). This mountain range forms the central, southern part of the African continental escarpment separating the Great Karoo from the Central Upper Karoo (Acocks 1953), and the buttress at Beaufort West also separates the Atlantic and Indian Ocean drainage systems. Mountains within the park rise to 920m above the plains and 1830m above sea level providing marked altitudinal zonation. Initially the park encompassed three farms: Stolshoek, Mountain View and Grootplaat. In 1983 another farm, Doringhoek, was included increasing the total extent of the conserved area to 330km$^2$; and in 1989 (during this study) a fifth farm,

University of Pretoria etd – Davies, R A G (1994)



Sandrivier, was purchased to extend the park in a westerly direction. Inclusion of these farms within the park marked the removal of domestic livestock and cessation of predator control programmes. Certain indigenous wild ungulates have been re-introduced, but stocking rates only approach estimated carrying capacity on the plain 'Lammetjiesleegte' near Beaufort West. While the park embraces some of the most spectacular scenery to be found in the Karoo, the predominance of mountainous habitat is not strictly representative of karoo veld and there are plans afoot to expand the park further to the west to encompass more plains habitat. Some of the mountainous habitat in the east may be exchanged for this land and the area known as Grootplaat is currently under negotiation. All analyses in this study include Grootplaat and exclude Sandrivier as parts of the park (unless otherwise stated). Restcamps and tarmac roads have only recently (1988) been established in the park to provide public access.

The KRNP was chosen as the core area in this study for a number of reasons. The park is one of the largest conserved areas in the Cape Karoo and is typical of mountainous habitat for the Nama-Karoo. In this way it is representative of rocky habitats on most karoo farmland. Vegetation in the park has enjoyed a significant respite from heavy grazing by livestock and is currently showing promising signs of recovery with a noticeable increase in grass cover (Novellie & van Heerden pers. comm.). Fairall (pers. comm.) noted how bare, eroding mountain slopes in the park have been stabilised by grass cover since proclamation of the park. Since 1979 predators such as caracals and black eagles have been unmolested, and this should have allowed these populations to settle down after the disruptive influence of removals. So the park afforded the opportunity of studying karoo processes under as natural conditions as possible. Furthermore, the abundance of rocky terrain in the park affords ideal habitat for both rock hyrax and black eagles, and there was no suggestion that the latter were limited by other factors such as the availability of nest sites. There were other logistical reasons for this choice of study site: facilities within the park and in Beaufort West nearby; easy access to neighbouring farmland; and a fairly central location in the Cape Karoo. This study also benefited from previous research conducted within the park, especially groundwork on the rock hyrax population (Fairall 1991, *in litt.*). Attempts to find other 'control areas' in the Cape Karoo where rock hyrax were free of predation by black eagles were unsuccessful. Accurate determination of hyrax numbers is very labour-intensive (Chapter 4) so these efforts were confined to a core area within the park to be thorough. But livestock predation by black eagles was assessed from nest studies outside the park and from visits to farms over a wide area of the Cape Karoo (see Chapter 11).

A detailed map of the park and surrounding areas (separating mountain slopes from plateaus and plains) can be found in Appendix 1. This map also shows road access from Beaufort West and a 1km numbered grid which has been used by other researchers in the park. Two substantial dolerite sills are exposed in the KRNP as a lower and upper escarpment. The lower escarpment at 310m above the plains has cliffs of up to 55m high and has become highly convoluted due to river incision. The upper escarpment at 920m above the plains has cliffs of up to 120m high and faces predominantly south. The rock on these cliffs crumbles easily and is not well suited for climbing. These sills are major features in the park and separate the topography into five major habitats: bottom plains, lower slopes, middle plateau, upper slopes and upper plateau (Fig. 4). For a cross-section through the underlying geology see Figure 5. The dramatic relief of the park is shown by a TIN model created from 100' contour lines off 1:50000 topocadastral maps using ARCINFO (Fig. 6). These figures are derived from a geographical information system of the habitats within the park which is fully explained in the next chapter.

University of Pretoria etd – Davies, R A G (1994)



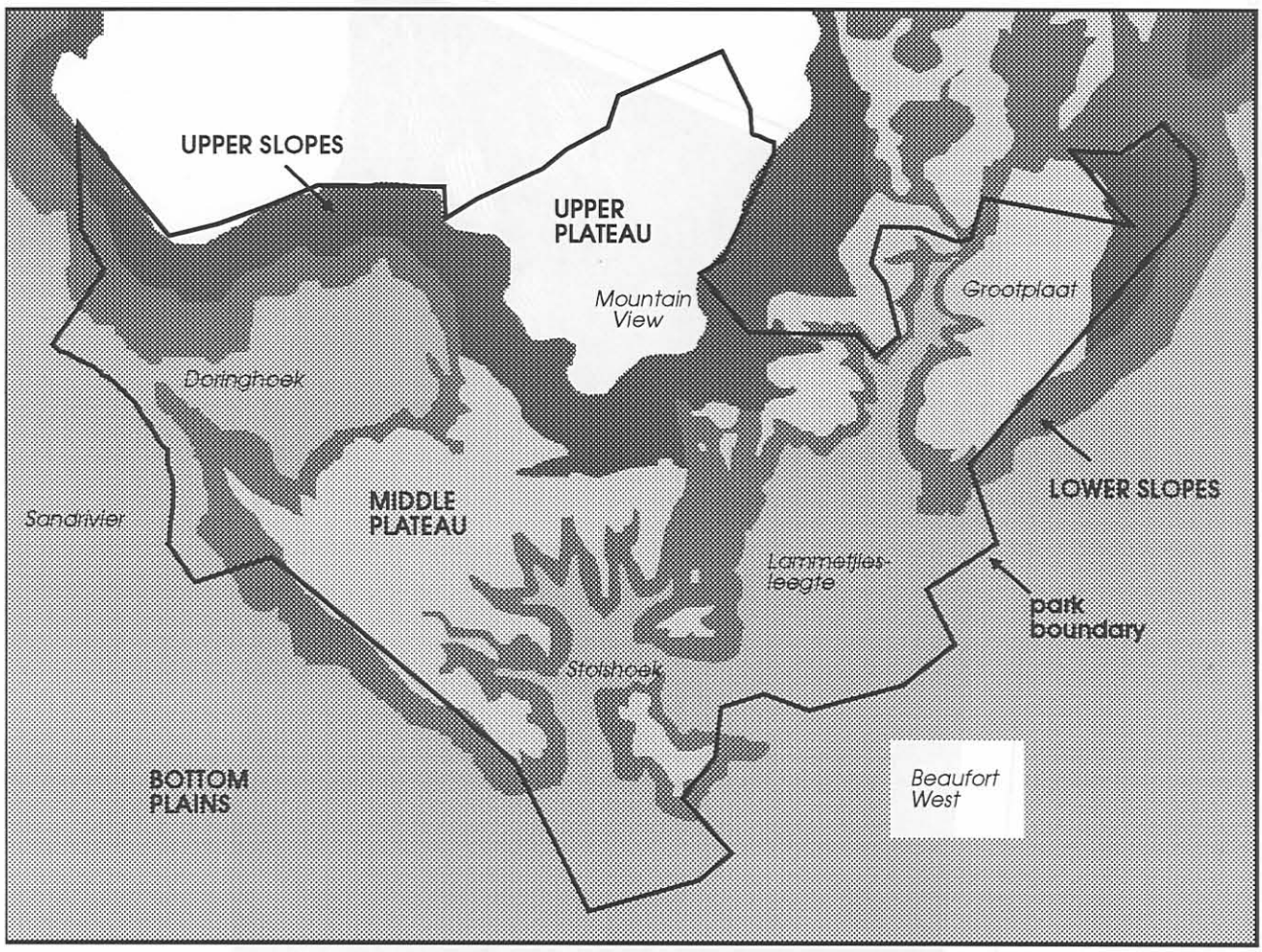



**Figure 4**. The Karoo National Park (KRNP) at Beaufort West and the major topographical habitats that it encompasses.

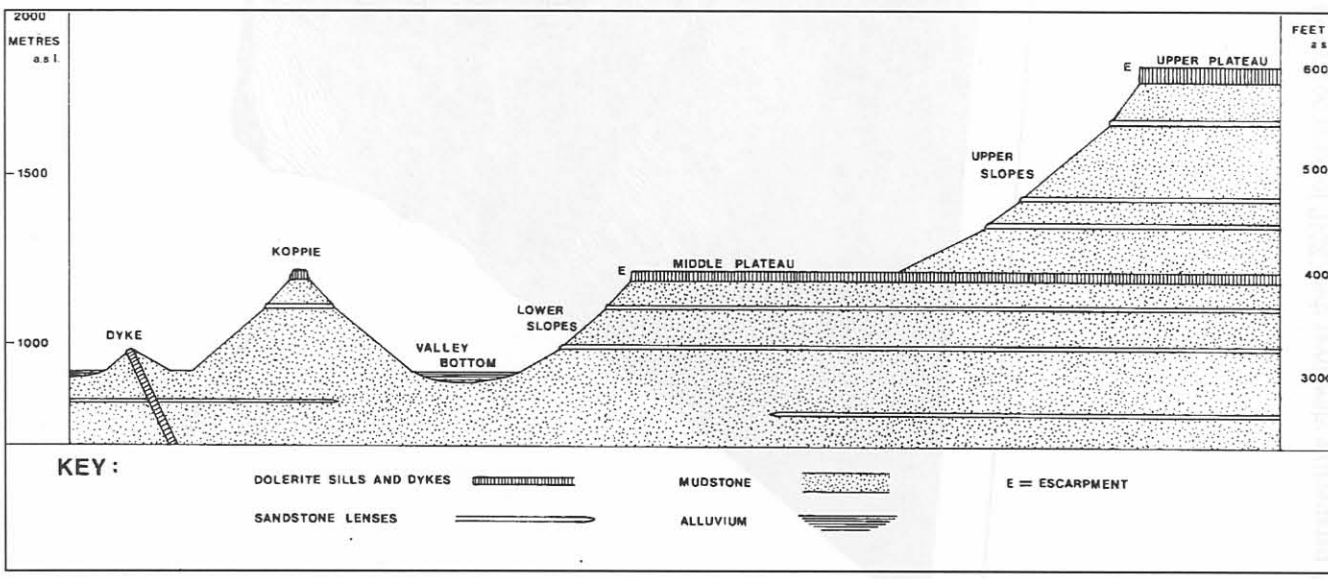



**Figure 5.** Cross-section through the Nuweveldberg in the KRNP (south to left; north to right) showing the underlying geology responsible for the topography.

University of Pretoria etd – Davies, R A G (1994)

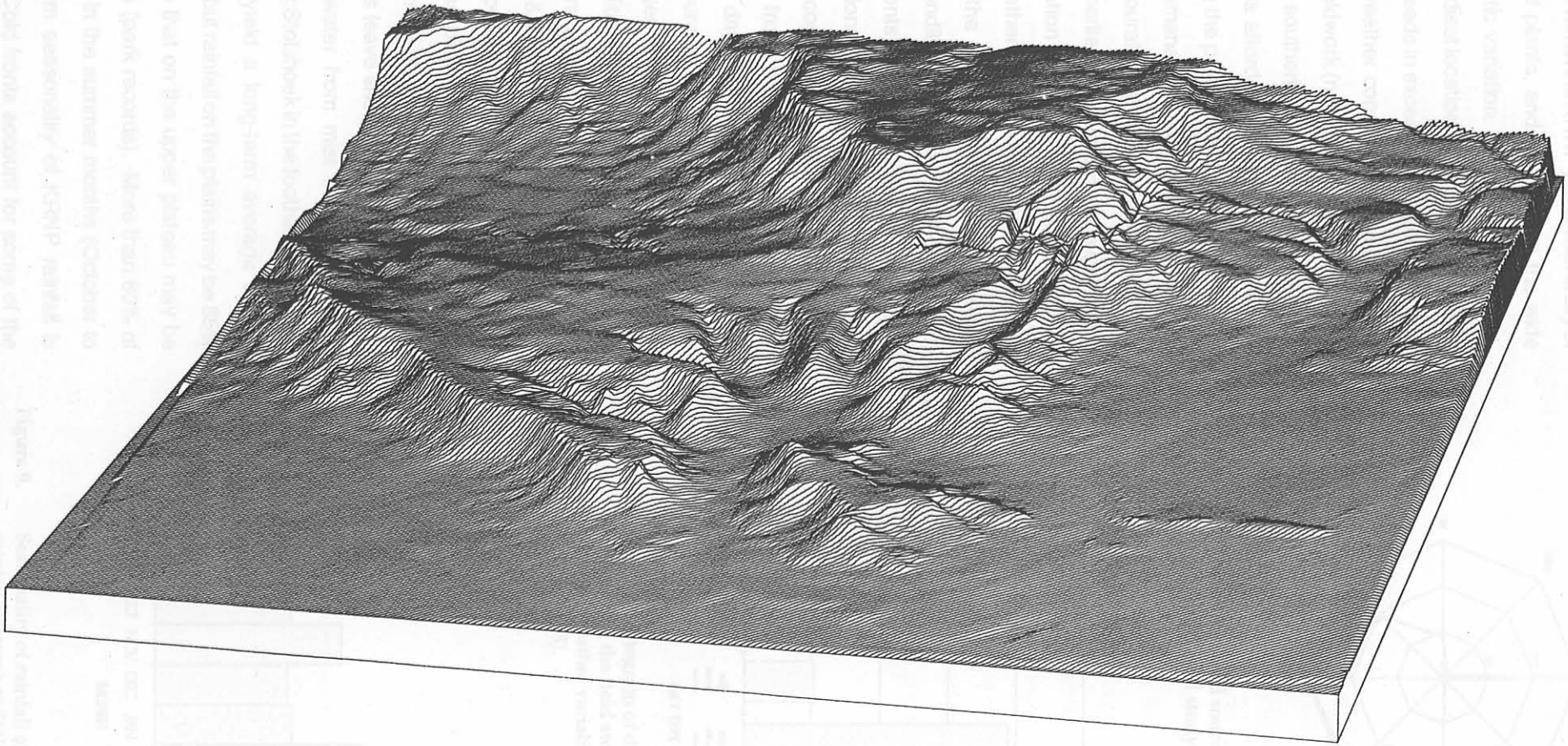




**Fig. 6.** A perspective view over the KRNP looking north-west clearly showing the eroded, plateau topography and the river incision into the lower escarpment. This 'TIN-model' was created by ARCINFO from 100' contour lines which were digitised for a geographical information system of park habitats (more details on methodology in the next chapter).

University of Pretoria etd – Davies, R A G (1994)



Altitudinal zonation within the KRNP yields a diversity of micro-habitats and plants, and encourages the wide and sudden climatic variation. Beaufort West is renowned as the windiest location in South Africa (Milford 1987) and wind speeds in excess of 170kph have been recorded. Daily weather conditions in the park were analysed during fieldwork (n=1250d) and revealed prevailing winds from southerly and south-easterly directions (Fig. 7). This affords ideal flying conditions for black eagles along the predominantly south-facing escarpments. Wind emanated mainly from the west or the east during behavioural observations (n=80d), with few southerlies or northerlies. Westerlies were significantly stronger. Correlation analyses were performed on important daily weather variables (full details in Chapter 8) and revealed the following: windy-sunny-warm (typical summer conditions) and windy/still-cloudy-cool (typical of cold fronts) were the most frequent daily weather combinations accounting for 65% days (see Fig. 8); still-sunny-cool days, which occur just after the passing of a cold front, were the least frequent day types; hot, sunny days were seldom windless; high atmospheric pressure was associated with cool, overcast days when gentle easterly winds brought high humidity; still conditions were much more prevalent in winter, but winds are generally strongest in the Karoo in September (Roux & Opperman 1986). Temperatures in the park can approach 45$^{o}$C on the low-lying plains in summer, but can plummet to -15$^{o}$C on the upper plateau with the arrival of a cold front in winter. Some of these cold fronts leave snow on the mountain tops, which also gain water from mist in the mornings. Rainfall records for Stolshoek in the foothills of the park kept since 1911 yield a long-term average annual rainfall of 270mm, but rainfall on the plains may be 85% of this value while that on the upper plateau may be 140% of this value (park records). More than 60% of these rains arrive in the summer months (October to March). Long-term seasonality of KRNP rainfall is shown in Fig. 9. Cold fronts account for some of the early summer rainfall component, but the bulk of the

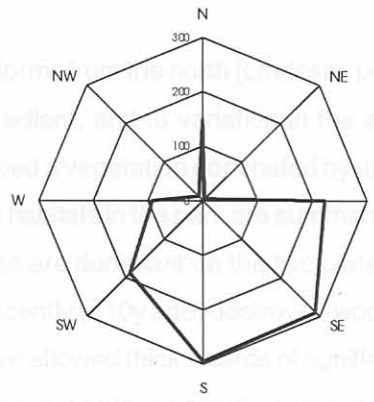



**Figure 7.** Prevailing wind sources in the KRNP during the field study (see text)

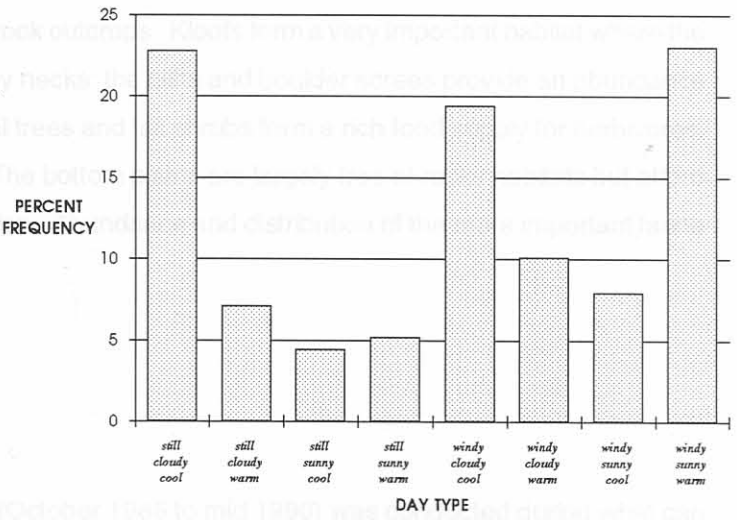



**Figure 8.** Frequency histogram of day types recorded in the KRNP during the field study in terms of three important weather variables (for method, see text and Chapter 8).

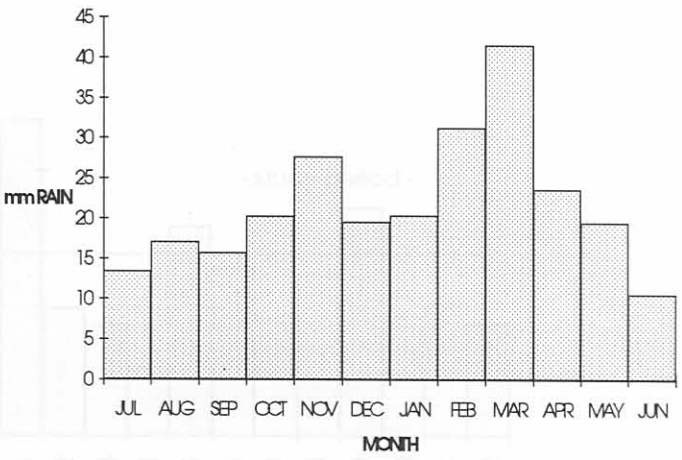



**Figure 9.** Seasonality of rainfall in the KRNP: monthly rainfall averages at Stolshoek determined for the period 1911 - 1982 (park records).

University of Pretoria etd – Davies, R A G (1994)



rain received is brought in late summer by anticyclonic tropical thunderstorms from the north (Lindesay pers. comm.). Vegetation cover in the park corresponds to the orographic rainfall gradient, and to variation in the alkaline soils (Webber 1989). High altitude conditions on the upper plateau have trapped a vegetation dominated by tussock grass and renosterbos. Full ecological descriptions of the major topographical habitats in the park are summarised in Table 1 to save lengthy description, and may be referred to for detail. Grasses are dominant on the two plateau habitats; on the sunny, northern aspects of the lower slopes; and where fire has recently (<10y ago) destroyed woody material. Good rainfall, low grazing pressure and the absence or rarity of fires have allowed thick swards of lignified grass and woody material to accumulate in some parts of the middle and upper plateaus, and these may be somewhat moribund. Riparian thickets comprising an overstory of subtropical trees and shrubs trace the courses of the episodic rivers. Rocky habitats are fully treated in the next chapter, but some details are given in Table 1. The majority of rocky habitats in the park are contained within the lower and upper slope macro-habitats (98% of screes; 84% linear outcrops), but substantial surface outcrops of the dolerite sills do occur on the plateau habitats. Certain flora (*Grewia robusta, Hermannia burkei*) are found in close association with rock outcrops. Kloofs form a very important habitat where the lower slopes and escarpment cliffs converge into valley necks: the cliffs and boulder screes provide an abundance of rock crevices; while a dense overstory of subtropical trees and tall shrubs form a rich food supply for herbivores. Kloofs may also provide important sources of water. The bottom plains are largely free of rocky habitats but afford good access to water courses and associated vegetation. Abundance and distribution of the more important fauna in the park are treated in Chapter 5.

*The period of study*

As mentioned earlier, the field research for this study (October 1986 to mid 1990) was conducted during what can be considered a period of recovery for karoo biota following a devastating drought in the early 1980's (Tyson 1983). KRNP rainfall data show that this drought was preceded by years of excellent rainfall prior to 1978 (Fig. 10), and this is in agreement with Tyson's (1986) 18y oscillation in the summer rainfall regions. The 3-4y rainfall pattern reported for Beaufort West is also apparent in these data. Stolshoek rainfall during the study period was just above the long-

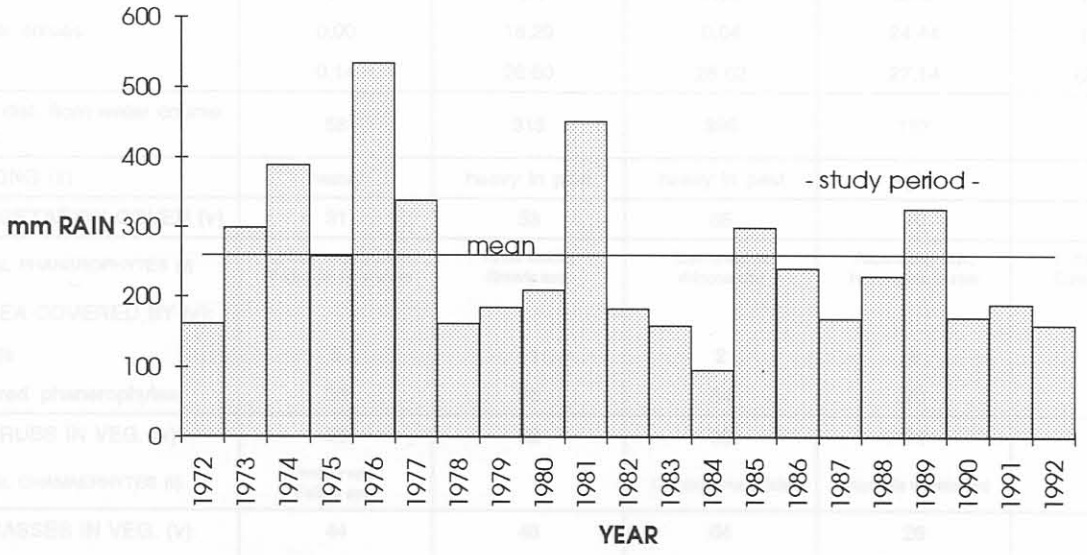



**Figure 10.** Annual rainfall (January to December) recorded at Stolshoek between 1972 and 1992.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 1

## ECOLOGICAL PHYSIOGNOMY OF THE MAJOR TOPOGRAPHICAL HABITATS WITHIN THE KAROO NATIONAL PARK

Sources: i - image analyser; ii - De Graaf, Robinson, van der Walt, Bryden & van der Hoven (1979); iii - park records; iv - Webber (1989); v - line transect sampling (Chapter 5) ; vi - ARCINFO geographical information system of the park (see Chapter 3). Statistical comparisons of habitat parameters (line-transect data) are presented on p. 69.

| ATTRIBUTE (& source) | BOTTOM PLAINS | LOWER SLOPES | MIDDLE PLATEAU | UPPER SLOPES | UPPER PLATEAU |
|---|---|---|---|---|---|
| EXTENT km2 (i) | 117,1 | 80,3 | 62,3 | 42,1 | 33,8 |
| ALTITUDE m a.s.l. (ii) | 910 | | 1220 | | 1830 |
| RELATIVE CLIMATE (ii) | arid hot | intermediate | intermediate | wet cool | wet cold |
| MIST, FROST & SNOW (ii) | rare | rare | rare | occasional | occasional |
| ANNUAL RAINFALL mm (iii) | 220 | 260 | intermediate | >350 | 360 |
| SLOPE ANGLE (deg.) (i) | 0 | 19 | 0 | 24 | 0 |
| ASPECTS (i) | - | convoluted | - | southerly | - |
| KLOOFS (i) | 0 | 10% area | 0 | 0 | 0 |
| SOILS (iv) | deep, light, sandy, loamy | shallow, stony (Swartland) | deep in places | shallow, stony | dark, moist |
| % AREA COVERED BY (v): | | | | | |
| bare ground | 90 | 1 | 13 | 0 | 20 |
| small, loose rocks | 10 | 55 | 70 | 56 | 54 |
| large, loose rocks | 0 | 28 | 5 | 39 | 13 |
| Mean dist. from outcrop m (v) | >1000 | 32 | 106 | 18 | 42 |
| DENSITY OF LINEAR ROCK OUTCROPS km/km2 (vi): | | | | | |
| dolerite escarpment | 0,00 | 1,70 | 0,24 | 0,96 | (0,24) |
| sandstone lenses | 0,34 | 2,98 | 0,09 | 2,53 | (0,09) |
| dolerite dykes | 0,06 | 0,23 | 0,05 | 0,23 | (0,05) |
| other | 0,02 | 0,09 | 0,01 | 0,00 | (0,01) |
| total | 0,42 | 5,00 | 0,39 | 3,73 | (0,39) |
| DENSITY OF 2D ROCK OUTCROPS ha/km2 (vi): | | | | | |
| surface outcrops | 0,00 | 0,04 | 27,63 | 0,03 | (27,63) |
| koppies | 0,00 | 0,52 | 0,35 | 0,00 | (0,35) |
| rocky screes | 0,14 | 7,75 | 0,60 | 2,65 | (0,60) |
| boulder screes | 0,00 | 18,29 | 0,04 | 24,44 | (0,04) |
| total | 0,14 | 26,60 | 28,62 | 27,14 | (28,62) |
| Mean dist. from water course m (v): | 58 | 313 | 395 | 157 | 189 |
| GRAZING (ii) | heavy | heavy in past | heavy in past | light | light |
| % VEGETATION COVER (v) | 31 | 53 | 65 | 70 | 78 |
| TYPICAL PHANEROPHYTES (ii) | Lycium oxycladum Rhigozum obavatum | Rhus lucida; Grewia spp. | Elytropappus rhinocerotis | Asparagus spp.; Hermannia burkei | E. rhinocerotis; Euryops annae |
| % AREA COVERED BY (v): | | | | | |
| thickets | 5 | 11 | 2 | 8 | 5 |
| scattered phanerophytes | 30 | 86 | 84 | 70 | 30 |
| % SHRUBS IN VEG. (v): | 56 | 52 | 36 | 74 | 40 |
| TYPICAL CHAMAEPHYTES (ii) | Pentzia spp.; Felicia spp. | | Chrysocoma ciliata | (macchia vegetation) | |
| % GRASSES IN VEG. (v): | 44 | 48 | 64 | 26 | 60 |
| TYPICAL GRASSES (ii): | annuals; perrenials v. scarce | Digitaria spp. Themeda trianda (esp. northerly aspects) | Aristida diffusa | few | Merxmuellera disticha (dominant tussock grass) |
| ALOES (ii): | Aloe claviflora | | A. broomii/ microstigma | A. striatula | |

University of Pretoria etd – Davies, R A G (1994)



term average. After reasonably good rains in 1985 and 1986 which broke the drought, conditions were relatively dry again for two consecutive summers, but became wetter during 1989, culminating in a bumper season of early summer rainfall towards the end of 1989 (Fig. 11). Beaufort West rainfall in November 1989 was the highest ever recorded for that month. This was a good rainfall event for most of the Karoo. Lesser kestrels *Falco naumanni* and wattled starlings *Creatophora cinerea* gathered in their thousands around Beaufort West at this time to feed on the locust swarms. This event was not followed up by good rains the following summer, and very dry conditions prevailed at the end of the field study. A chronological plan of the research is presented in Fig. 12 for reference purposes.

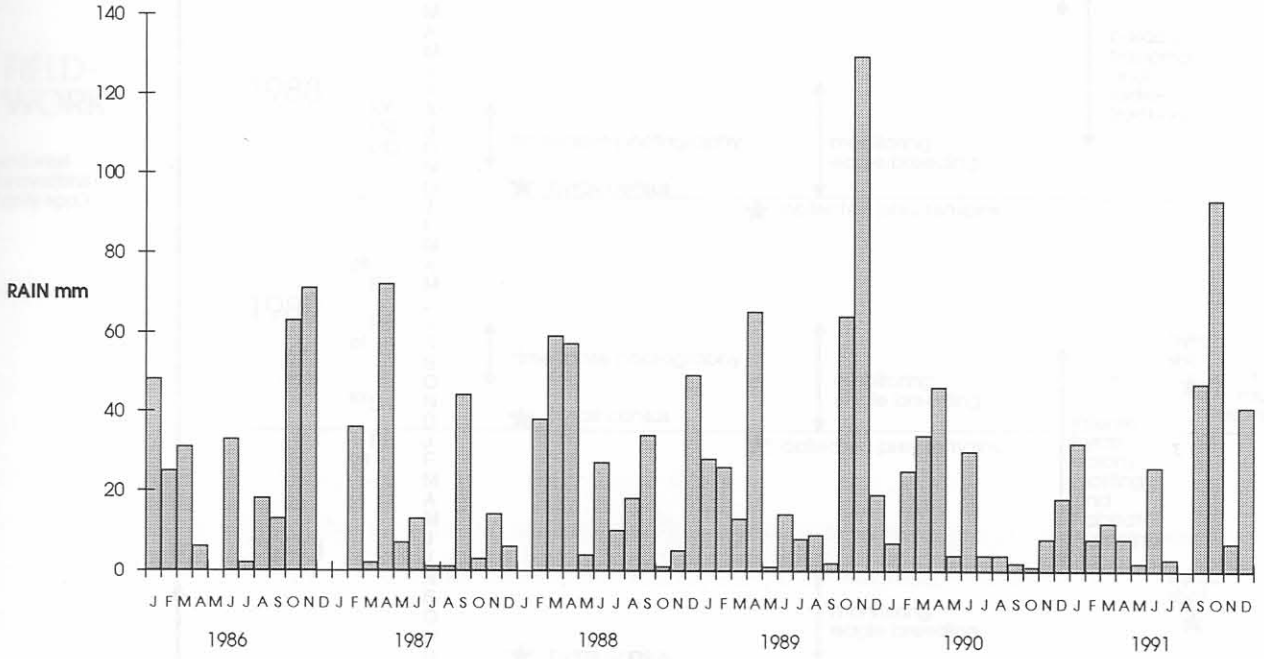



**Figure 11.** Monthly rainfall recorded at Stolshoek over the study period.

*Previous, relevant research*

Although black eagles had not been researched in the KRNP prior to this study, Fairall (1991, *in litt.*) and workers had done some important monitoring of the hyrax population. Counts at two colonies suggested a four-fold decline in numbers between 1981 and 1985 (Fig. 13). This was part of a more widespread population decline described earlier. The current study was thus carried out at a time when prey density was low and may have been well below the carrying capacity of the rocky environment for small herbivores. This has an important bearing on the study because numerous field studies have indicated that predation pressure is generally greatest when prey are at low density (e.g. Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Henttonen 1985; Newsome, Parer & Catling 1989; Sinclair, Olsen & Redhead 1990; Boutin 1992; Pech, Sinclair, Newsome & Catling 1992). Population data were also available for ungulates in the park (including small antelope) from annual helicopter censuses conducted by the National Parks Board since 1987

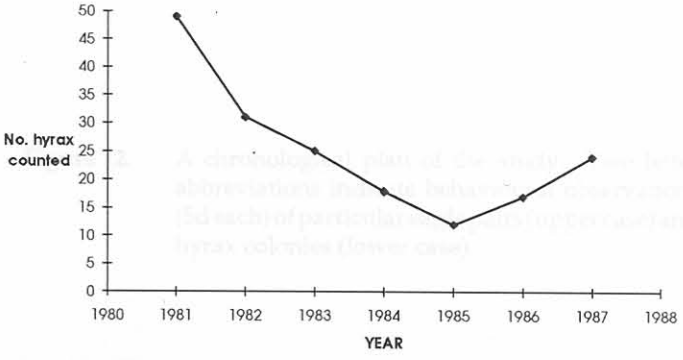



**Figure 13.** Number of hyrax counted at two colonies (combined) in the KRNP (prior to this study) by Fairall *(in litt.)*

2021021
282706

University of Pretoria etd – Davies, R A G (1994)



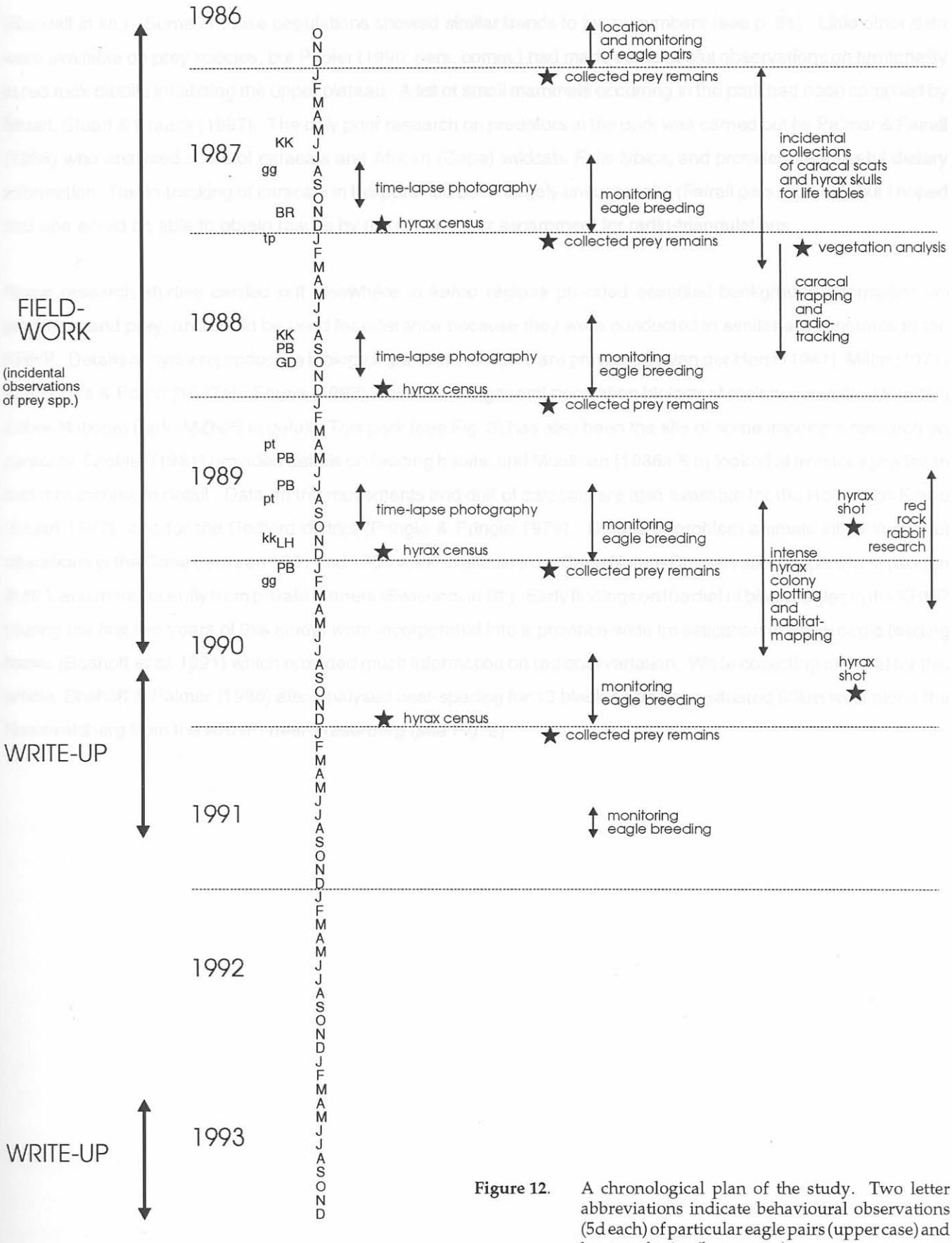



**Figure 12.** A chronological plan of the study. Two letter abbreviations indicate behavioural observations (5d each) of particular eagle pairs (upper case) and hyrax colonies (lower case).

University of Pretoria etd – Davies, R A G (1994)



(Randall *in litt.*). Some of these populations showed similar trends to hyrax numbers (see p. 81). Little other data were available on prey species, but Pepler (1990; pers. comm.) had made some useful observations on territoriality in red rock rabbits inhabiting the upper plateau. A list of small mammals occurring in the park had been compiled by Stuart, Stuart & Braack (1987). The only prior research on predators in the park was carried out by Palmer & Fairall (1988) who analysed scats of caracals and African (Cape) wildcats *Felis lybica*, and provided very useful dietary information. Radio-tracking of caracals in the park had been largely unsuccessful (Fairall pers. comm.), but I hoped that one would be able to obtain results by using the upper escarpment for radio-triangulations.

Some research studies carried out elsewhere in karoo regions provided essential background information on predators and prey, and could be used for reference because they were conducted in similar environments to the KRNP. Details of hyrax reproductive biology in parts of the Karoo are provided by van der Horst (1941), Millar (1971) and Fourie & Perrin (1987a). Fourie (1983) looked at the general population biology of rock hyrax in the Mountain Zebra National Park (MZNP) in detail. This park (see Fig. 3) has also been the site of some important research on caracals: Grobler (1981) provided details on feeding habits; and Moolman (1986a & b) looked at livestock predation and movements in detail. Data on the movements and diet of caracals are also available for the Robertson Karoo (Stuart 1982), and for the Bedford district (Pringle & Pringle 1979). Details of problem animals killed in control operations in the Cape between 1931 and 1955 were available from Cape Nature Conservation Department (Norton *in litt.*), and more recently from private farmers (Swiegers *in litt.*). Early findings on the diet of black eagles in the KRNP (during the first two years of this study) were incorporated into a province-wide investigation of black eagle feeding habits (Boshoff *et al.* 1991) which provided much information on regional variation. While collecting material for this article, Boshoff & Palmer (1988) also analysed nest-spacing for 13 black eagle pairs situated 80km west along the Nuweveldberg from the KRNP, near Fraserberg (see Fig. 3).

University of Pretoria etd – Davies, R A G (1994)



CHAPTER 3

# THE REFUGE RESOURCE

## INTRODUCTION

The significance of refuge in mediating predator-prey interactions was appreciated early on in the development of predator-prey theory and empiricism. When Gause (1934) introduced prey refuge into his *Didinium* - *Paramecium* experiments he reversed the outcome of these experiments, with the prey surviving extinction. By protecting some prey, refuge eliminates one of two ways in which predator-prey interactions may collapse (Taylor 1984), and has generally been found to confer stability on predator-prey experiments in the laboratory (e.g. Flanders 1958; Flanders & Badgley 1963). But this stability is dependent on the effectiveness of the refuge (White & Huffaker 1969). Spatial heterogeneity offers transient refuge to prey in such experiments especially if predators tend to aggregate in areas of high prey density and if their movements are less effective than those of their prey (Pimentel, Nagel & Madden 1963; Hastings 1977; Takafuji 1977; Maly 1978). Most laboratory experiments indicated increased stability with increased spatial heterogeneity (Huffaker 1958; Huffaker, Shea & Herman 1963). Diffusion models have predicted that such spatial heterogeneity may arise endogenously from the interaction if an homogenous environment is sufficiently large (McMurtrie 1978; Hilborn 1979).

In agreement with laboratory experiments, factors representing protection for a fraction or a number of prey were found to confer stability upon early predator-prey models such as the Lotka-Volterra and Nicholson-Bailey models (Leslie & Gower 1960; Bailey, Nicholson & Williams 1962; St Amant 1970; Hassell & May 1973) - greater stability being conferred when a fixed number rather than a fixed proportion of the prey was protected (Hassell 1976). In the case of prey moving randomly between refuge and hostile environments, diffusion models predict that interactions can only be stable if the refuge habitat exceeds a minimum critical size (Kierstead & Slobodkin 1953; Gurney & Nisbet 1975). But the early predator-prey models have been found to be inherently unstable and biologically unrepresentative in some important regards. It is now preferred to model the predator functional response on predator-prey ratios (*per capita* resources) rather than simply prey density (Berryman 1992; Slobodkin 1992), especially for heterogeneous environments (Arditi & Saïah 1992) with enrichment. Ratio-dependent theory has also demonstrated the importance of refuge, and generally affords a better fit to field situations (marriage between theoretical and empirical studies of predation has been a problem in the past, see Hansson 1988a). Akçakaya (1992) used ratio-dependence between predator, prey and food resources together with a simple refuge factor to correctly predict the periodicity and amplitude of snowshoe hare *Lepus americanus* cycles.

Field studies do not always indicate that prey refugia confer stability on interactions. In fact there is mounting evidence that refuge can give prey populations the advantage, certainly in relatively simple ecosytems, leading to oscillations (limit cycles) and sometimes destructive interaction between prey populations and their food resources. Vole cycles in northern Europe show a clear positive correlation with snow cover which protects increases in vole populations from an immediate response by generalist predators but not from a delayed response by specialist mustelids (Hansson & Henttonen 1985; Hansson 1988b). Likewise, dense stands of spruce *Picea mariana* and willow *Salix* spp. or alder

University of Pretoria etd – Davies, R A G (1994)



*Alnus* spp. thickets afford refuge to snowshoe hares in a habitat mosaic, permitting population increase before the obligate predators such as Canadian lynx *Lynx canadensis* catch up with the changes in hare density (Wolff 1980). Reluctance of spotted hyenas to enter bush and woodland following migrating Serengeti wildebeest and a consequent low ratio of predator to prey in this region may be responsible for occasional destructive interaction between wildebeest and their food resources in the Serengeti (Kruuk 1970, 1972a).

Prey refuges can take many forms in nature, but refuge to one prey may have the opposite effect for another. Snow protects voles and lemmings from raptors but it renders large ungulates more vulnerable to attack by wolves (Nelson & Mech 1986) - and the behavioural response to this vulnerability is an increase in group size (Heard 1992; Jedrzejewski, Jedrzejewski, Okarma & Ruprecht 1992). Like snowshoe hares, hazel grouse *Bonasa bonasia* favour densely-vegetated habitats for protection from goshawk *Accipiter gentilis* attack (Lindén & Wikman 1983). Grass rats *Arvicanthis blicki* in Kenya also find refuge in dense vegetation but population irruptions may lead to these rodents eating down their refuge and exposing themselves to heavy predation (Brown 1976, p. 105). Australian house mice *Mus domesticus* minimise predation risk by favouring protective habitats especially on moonlit nights, but they do not show this behaviour in areas where predators are absent (Dickman 1992). Increased exposure of prey when vegetation cover is thin during the dry season has been offered as an explanation for the timing of raptor breeding seasons in Africa (Moreau 1950). So refuge may have far-reaching consequences on the behaviour of both prey and predator. Herrera and MacDonald (1989) suggest that ponds on Venezuelan floodplains afford protection from predators and a rich food supply worth defending to capybaras *Hydrochoerus hydrochaeris*, and this has led to territorial behaviour by groups in this species. Territorial behaviour is also evident in lagomorphs that use cover, particularly those unable to create their own burrows (Cowan & Bell 1986; Brown, Southwick & Golian 1989). Many small mammals, especially rodents, are able to modify their environment and create refuge by burrowing. But burrows are not very permanent features and are not always effective at preventing predation, especially in soft substrates (Myers & Parker 1975; Murie 1992). Habitats which afford good protection from predators are often occupied by more dominant individuals in a prey population, forcing subordinates into suboptimal, risky buffer zones (Jenkins, Watson & Miller 1964; Bigalke 1970). The concept of a displaced, vulnerable component of the prey population confers stability to predator-prey models (Smith 1972; Jones 1978). Besides using spatial refuges, many prey populations find refuge in time. Synchronised breeding confers safety in numbers to the highly vulnerable juveniles of many animals (e.g. Murie 1944; Kruuk 1970, 1972a; Hughes & Richard 1974), and certain vulnerable insect imagos (Lloyd & Dybas 1966a&b).

Rock hyrax in the Karoo show a distinct birth-pulse, mostly in November (Millar 1971; Fourie 1983), and this suggests that the juveniles might be heavily hunted because synchronised breeding is not usually expected in unpredictable environments. Rock hyrax are extremely refuge-dependent in space. Their refuge normally takes the form of crevices in rock outcrops and boulder screes, and has been described superficially by Turner & Watson (1965), George & Crowther (1981), Hoeck (1982), Fourie (1983), and in some detail by Sale (1966a). The minimum size for crevices used by hyrax appears to be set by the size of the animals (George & Crowther 1981), while large crevices which would permit entrance of felid predators are avoided (Sale 1966). Besides rock outcrops, hyrax have been observed to use dongas, stone walls, culverts under roads, and the burrows of suricates *Suricata suricatta* and aardvarks during population irruptions (Thomas 1946). Rock hyrax are nearly always seen in very close proximity to their refuges and

University of Pretoria etd – Davies, R A G (1994)



minimise the time they spend foraging away from the rocks (Sale 1965; Turner & Watson 1965; Fourie 1983). Dispersion often occurs at night (A. Root & R. Pellow in Hoeck 1982; pers. obs.). Besides protection from predators, rock crevices afford a comfortable microclimate to hyrax (Turner & Watson 1965; Sale 1966a; Fourie 1983). Rock hyrax are thermally labile - they can allow their body temperature to drop by a few degrees at night and then use the microclimates around their refuge resource to thermoregulate during the day (Sale 1970b; Louw 1971; Louw, Louw & Retief 1972; McNairn & Fairall 1984). The first few hours of every morning are usually spent 'sunning' on the rocks, especially on karoo winter days (Fourie 1983).

Refuge used by rock hyrax is unusual in comparison with other forms of refuge used by smaller mammals for the following reasons: it is relatively permanent; it cannot be modified by the animals; it provides shelter for a fixed number of individuals; it is highly effective against nearly all predators; and it occurs in an extensive and patchy distribution within mountainous habitats. For these reasons, rocky refuges can be expected to confer a very real measure of K or carrying capacity on the landscape for hyrax populations, and a high degree of stability on the interaction between rock hyrax and their predators. Although rocky habitats afford hyrax with safe access to a fixed area of vegetation, the number of hyrax that this food resource should support might vary with the effects of enrichment by rainfall. Allan (1988) speculated that a pattern of poor breeding by black eagles in wet years and good breeding in dry years might reflect the distance that hyrax must venture from refuges to feed and thus their vulnerability to predation. Previous population models of rock hyrax (Fairall, Vermeulen & van der Merwe 1986; Swart *et al.* 1986) make the simple assumption that hyrax are protected at low densities and vulnerable at high densities. For modelling to accurately reflect hyrax populations in the Karoo I felt that accurate measurement of the refuge resource (this chapter) and accommodation of the effects of rainfall enrichment (see Chapter 12) would be essential.

While the significance of refuge is widely accepted in theory, its influence in field situations is not yet fully understood (Crawley 1992: p. 487). To compare empirical observations on the influence of refuge to rock hyrax with theoretical predictions introduced above, a detailed study of the refuge resource was warranted (it should be noted that the same refuge resource is also used by red rock rabbits and by black eagles for nest sites). I also hoped that by studying the densities of hyrax in sample units of rocky habitat, I would be able to extrapolate a population estimate of hyrax in accordance with the extent of these habitats. A general description of the nature and origins of karoo rocks was given in Chapter 2. This chapter provides a detailed description and analysis of the refuge micro-habitats found in the KRNP. The relationship of prey and predator to these habitats is examined in later chapters.

University of Pretoria etd – Davies, R A G (1994)



## METHODS

*Categorization of refuge habitats*

Rocky habitats in the KRNP can be broadly divided into 'lineal' outcrops such as escarpment which are clearly distributed along one dimension, and 'areal' habitats such as screes which are clearly distributed in two dimensions. The principal rocky and other microhabitats that potentially afford shelter to rock hyrax (Figure 14) were further classified as follows in terms of substrate, form, situation and distribution. Dykes are lineal habitats and derive from vertical dolerite intrusions where the substrate has been exposed as strings of discontinuous (scattered) knobs. Horizontal dolerite intrusions, known as sills, are more common (98% by area of outcrop). The tops of sills can be exposed in an areal fashion either as discontinuous knobs on the surface of plateaus (surface outcrops), or as small continuous (solid) caps protecting cones of shale bedrock (koppies). Particularly large outcrops of rock are exposed in a lineal fashion at the edge of the dolerite sills. Most of these 'escarpment' outcrops are dolerite but sandstones may also be exposed, especially at the base of large cliffs. Some deflected dolerite sills may also be exposed just above or below the escarpment edge. These variants are all considered escarpment. Sheer cliffs of dolerite weather along perpendicular cooling joints - with time this 'columnar weathering' may produce an alignment of tall pillars which may erode further to form a discontinuous string of knobs. Escarpment outcrops may occur in any one of these three lineal forms. Horizontal sandstone lenses in the KRNP are either exposed on slopes or by river action on the bottom plain, as lineal outcrops of continuous rock surface. They can be broadly separated into tall cliff-like outcrops (where vertical planes > horizontal planes) or flat outcrops (where horizontal planes > vertical planes). The latter usually occur on gentler slopes. Weathering of dolerite sills and sandstone lenses produces screes on the slopes immediately

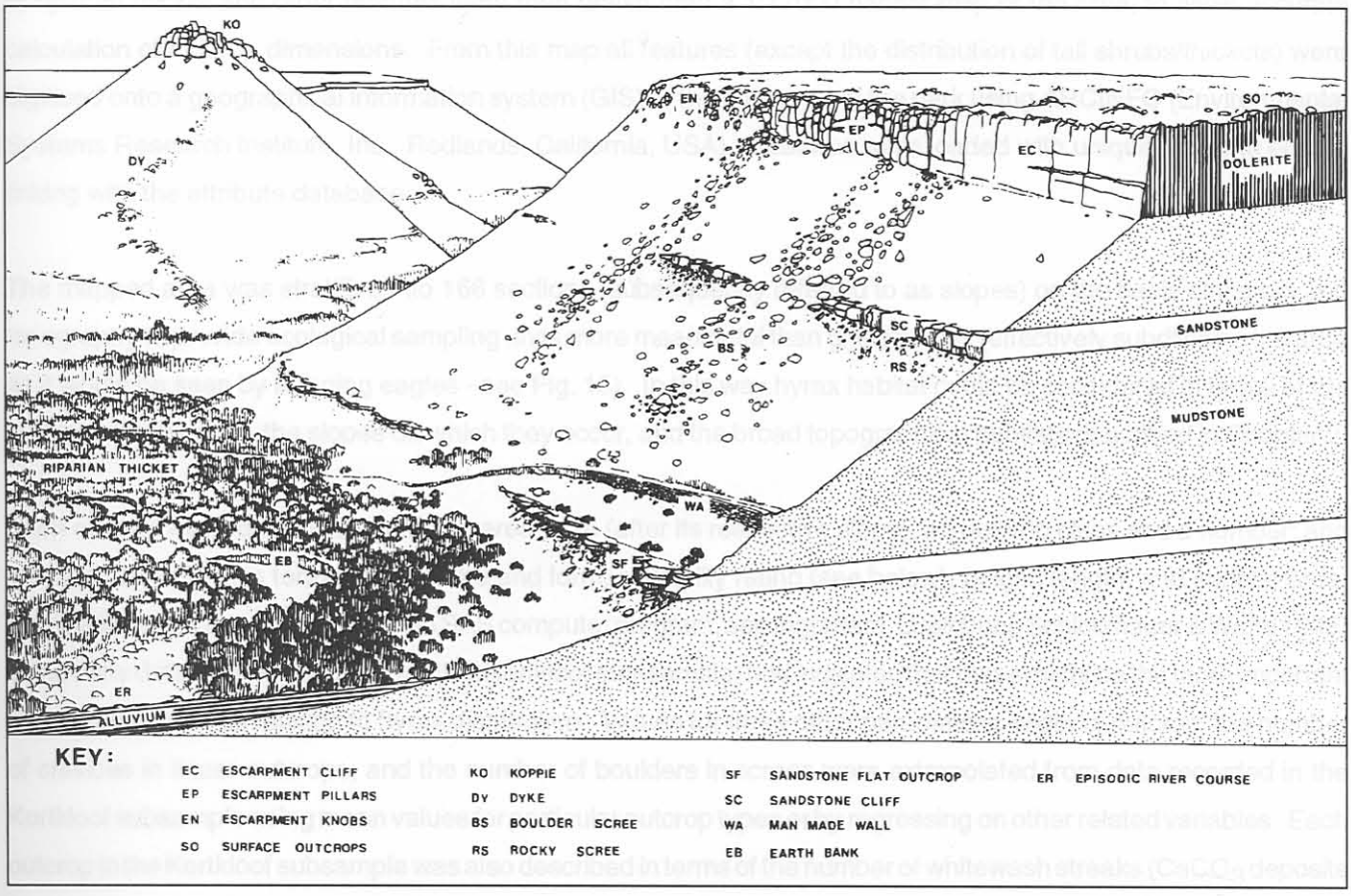



**Figure 14.** A detailed topographical diagram of the KRNP illustrating the classes of refuge micro-habitats available to rock hyrax, and the substrates from which they derive.

University of Pretoria etd – Davies, R A G (1994)



beneath these outcrops. Screes can be defined as discernible clusters of loose rocks and have a discontinuous, areal distribution. Rocky screes (most rocks <0,7m high) usually derive from the sandstone outcrops. Boulder screes (most rocks >0,7m high) nearly always derive from the larger escarpment outcrops. Sandstone rocks are used in the construction of lineal walls for roads and kraals which can afford refuge to hyrax. Alluvium is exposed as small lineal cliffs and banks along river courses in valley bottoms and it is also used in the construction of dam walls. All potentially afford refuge to hyrax.

---

*Habitat mapping*

Detailed habitat-mapping was conducted over 136km$^2$ of the Nuweveld mountains and surrounding plains. Compensation for the angle of lower slopes increased these surface areas by 5,8%; while compensation for the angle of upper slopes increased these surface areas by 9,6%. So the total mapped area represents 139km$^2$ of real surface area. This area encompassed four complete black eagle territories, and parts of four other adjacent territories (Chapter 6). Every rock outcrop (n=3365) within this area was viewed and outlined on 1:10000 aerial photographs of the region (supplied by International Aviation Services Pty. Ltd., Pretoria). Each outcrop was numbered and described in terms of various parameters and these details were then loaded onto an attribute database (details below). The aerial photographs were subject to distortion, so a 500m grid was superimposed onto the photographs from 1:50000 topocadastral maps of the area using various landmarks. The rock outcrops, water courses, stretches of riparian thicket and other features were then drawn onto a 1:17000 habitat map of the area, to allow accurate calculation of outcrop dimensions. From this map all features (except the distribution of tall shrubs/thickets) were digitised onto a geographical information system (GIS) of the core area of the park using ARCINFO (Environmental Systems Research Institute, Inc., Redlands, California, USA). Features were loaded with unique labels to enable linking with the attribute database.

The mapped area was stratified into 166 sections (subsequently referred to as slopes) on the basis of aspect and topography to provide ecological sampling units more meaningful than grid squares (effectively subdividing the area as it would be seen by foraging eagles - see Fig. 15). In this way hyrax habitat could be considered in terms of the outcrops themselves, the slopes on which they occur, and the broad topographical habitats described in Chapter 2.

Each outcrop mapped was assigned an area code (after its respective slope), an outcrop class and a number; and was then described in terms of substrate and form, suitability rating (see below), height, length, and surface area. Correlation analyses ($R^2$ option in the SAS computer program, see Ingraham, Luginbuhl, Schlotzhauer & Watts 1988) on an early database of 786 outcrops (the Kortkloof sub-sample) had indicated that these might be the more important descriptive variables relating to hyrax distribution. Values for three other parameters: width of outcrop; the number of crevices in linear outcrops; and the number of boulders in screes were extrapolated from data recorded in the Kortkloof subsample using mean values for particular outcrop types or by regressing on other related variables. Each outcrop in the Kortkloof subsample was also described in terms of the number of whitewash streaks ($CaCO_3$ deposits from hyrax urine), and an index of the local density of large shrubs.

University of Pretoria etd – Davies, R A G (1994)

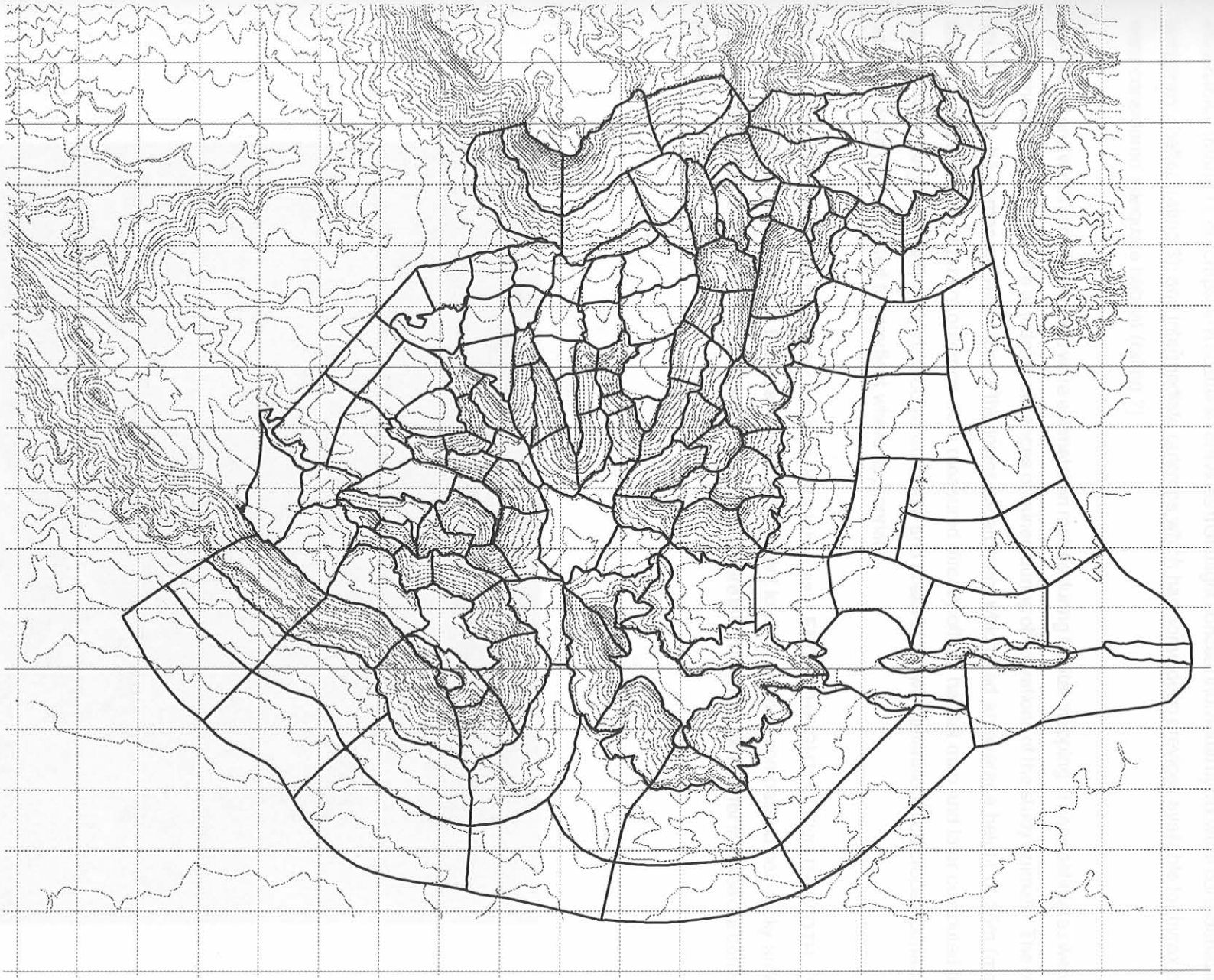


**Figure 15.** The area within the Karoo National Park where detailed habitat mapping was conducted and its subdivision into slopes (1km grid and 100' contours shown)

University of Pretoria etd – Davies, R A G (1994)



The suitability rating of an outcrop was assessed rather subjectively in terms of the nature and extent of the shelter that it appeared to afford to hyrax: outcrops with an abundance of deep crevices and fissures were considered to be ideal habitat (rating 1); outcrops with scattered crevices that might conceal individual hyrax were considered to afford temporary shelter (rating 3); and intermediate outcrops which had some deep crevices available for hyrax colonies were considered adequate habitat (rating 2).

The height and width of rock outcrops were estimated in metres during habitat mapping. These estimates were drawn from considerable experience at judging distances obtained during observations of the study animals. The outcrops could usually be compared with cliffs of the lower escarpment which had an average height of 35m (measured directly). Widths of escarpment outcrops were measured directly off the habitat map and later computed from the GIS, as were lengths of all linearly-distributed outcrops, and areas of all two-dimensional outcrops. Dimensions of outcrops were compensated for gradient where appropriate.

Surface areas for the continuous linear habitats were taken as: LENGTH*HEIGHT + LENGTH*WIDTH. Surface areas for the discontinuous linear habitats (dykes; escarpment knobs) which encompassed non-rocky areas were taken simply as LENGTH*WIDTH. Surface areas of koppies were taken from the formula for the area of a demisphere: $(\pi d^2)*0,5$



University of Pretoria etd – Davies, R A G (1994)



# RESULTS AND DISCUSSION

## *Extent and distribution of refuge micro-habitats*

The distribution of the major classes of rocky habitats is shown in Figure 16 for the mapped area of the park. The distribution of episodic water courses (drainage routes) is shown in Figure 17 for the same area. Riparian thickets growing along these water courses provide important feeding habitat for hyrax as well as some protection from eagles (Chapter 4). Good access to this habitat is found on the slopes and bottom plains, but not on the middle plateau. It is evident that availability of rock outcrops varied markedly between the major topographical habitats (Fig. 16). Densities of the main outcrop types in the different topographical habitats are illustrated in Figure 18 (data given in Table 1, page 20; statistical comparisons presented on page 69). All mountain slopes in the mapped area have consistently high densities of rock outcrops, and these major habitats account for 84% of all lineal outcrops by length and 98% of all screes by area. The distribution of lineal outcrops within lower and upper slopes are basically similar, but upper slopes (being less convoluted and steeper) contain relatively shorter stretches of very tall escarpment outcrops which have resulted in high densities of boulder scree. All outcrop types are scarce on the plains and plateaus except for surface outcrops which occupy a significant area of the middle plateau. The upper plateau (not mapped) is very similar to the middle plateau and is also characterised by surface outcrops of dolerite.

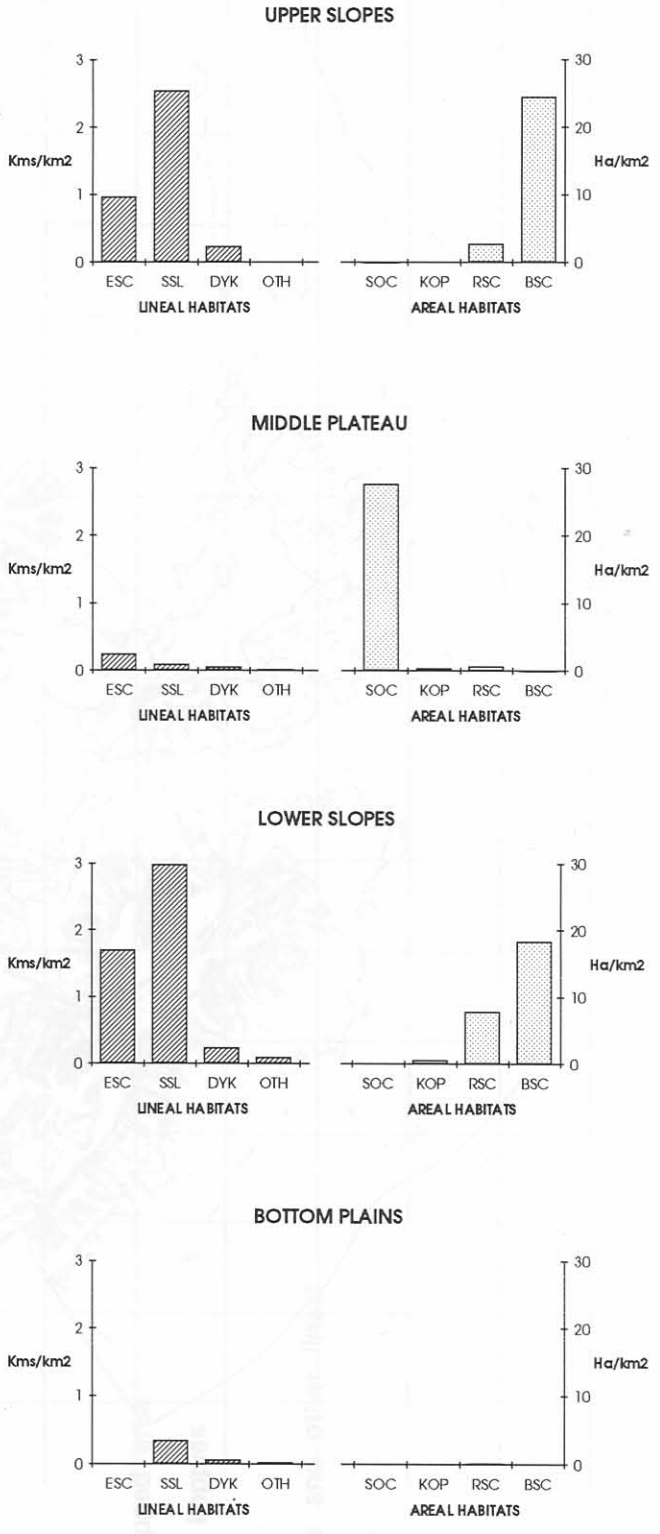



**Figure 18.** Densities of the principal refuge micro-habitats in the major topographical habitats of the Karoo National Park. Lineal and areal habitats had to be shown on separate scales. KEY: ESC escarpment, SSL sandstone lenses, DYK dykes, OTH other lineal outcrops, SOC surface outcrops, KOP koppies, RSC rocky screes, BSC boulder screes.

University of Pretoria etd – Davies, R A G (1994)

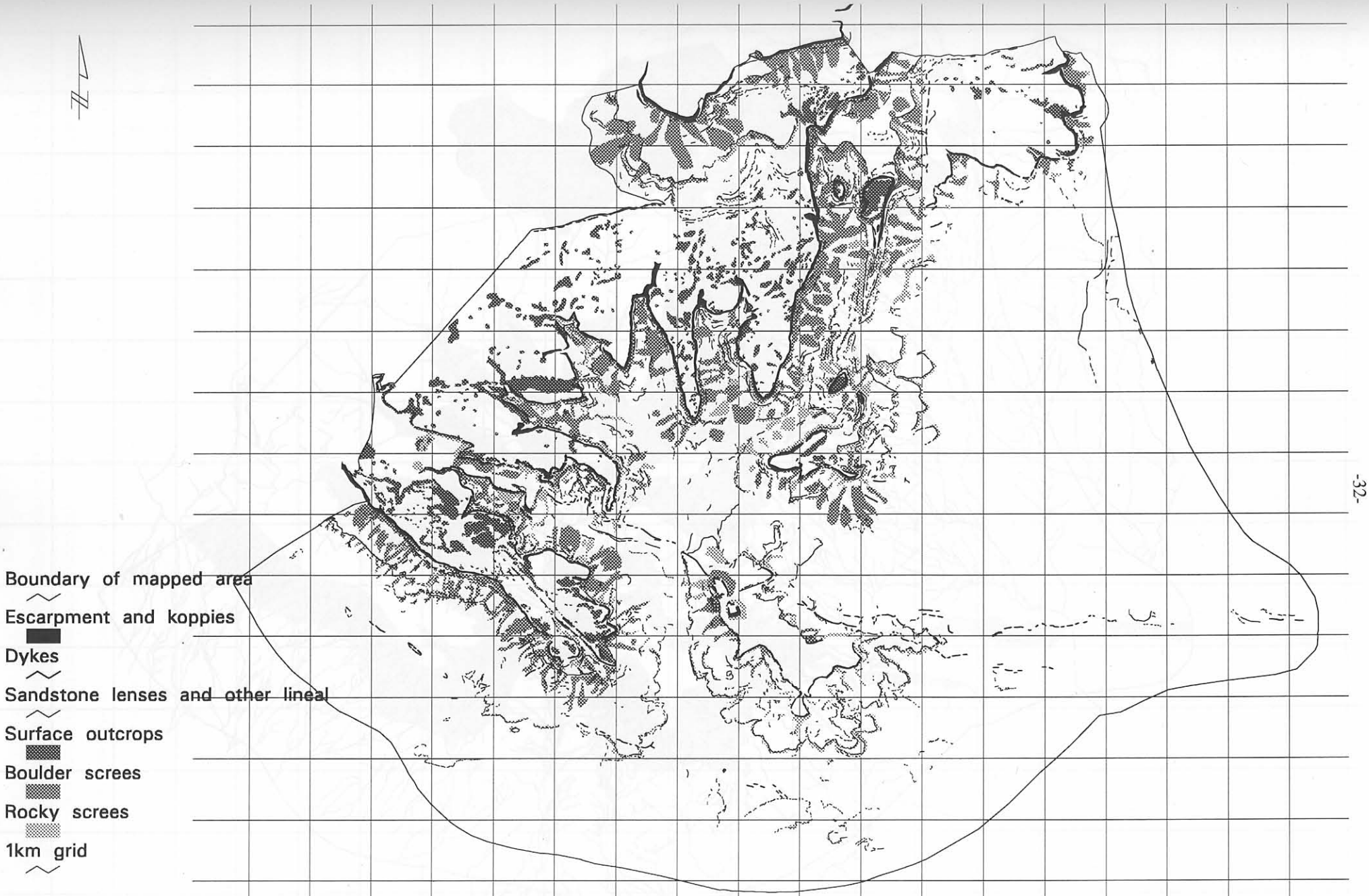



**Figure 16.** Geographical information system of the principal refuge micro-habitats within the Karoo National Park (1km grid shown) generated from ARCINFO coverages using ARCVIEW

University of Pretoria etd – Davies, R A G (1994)

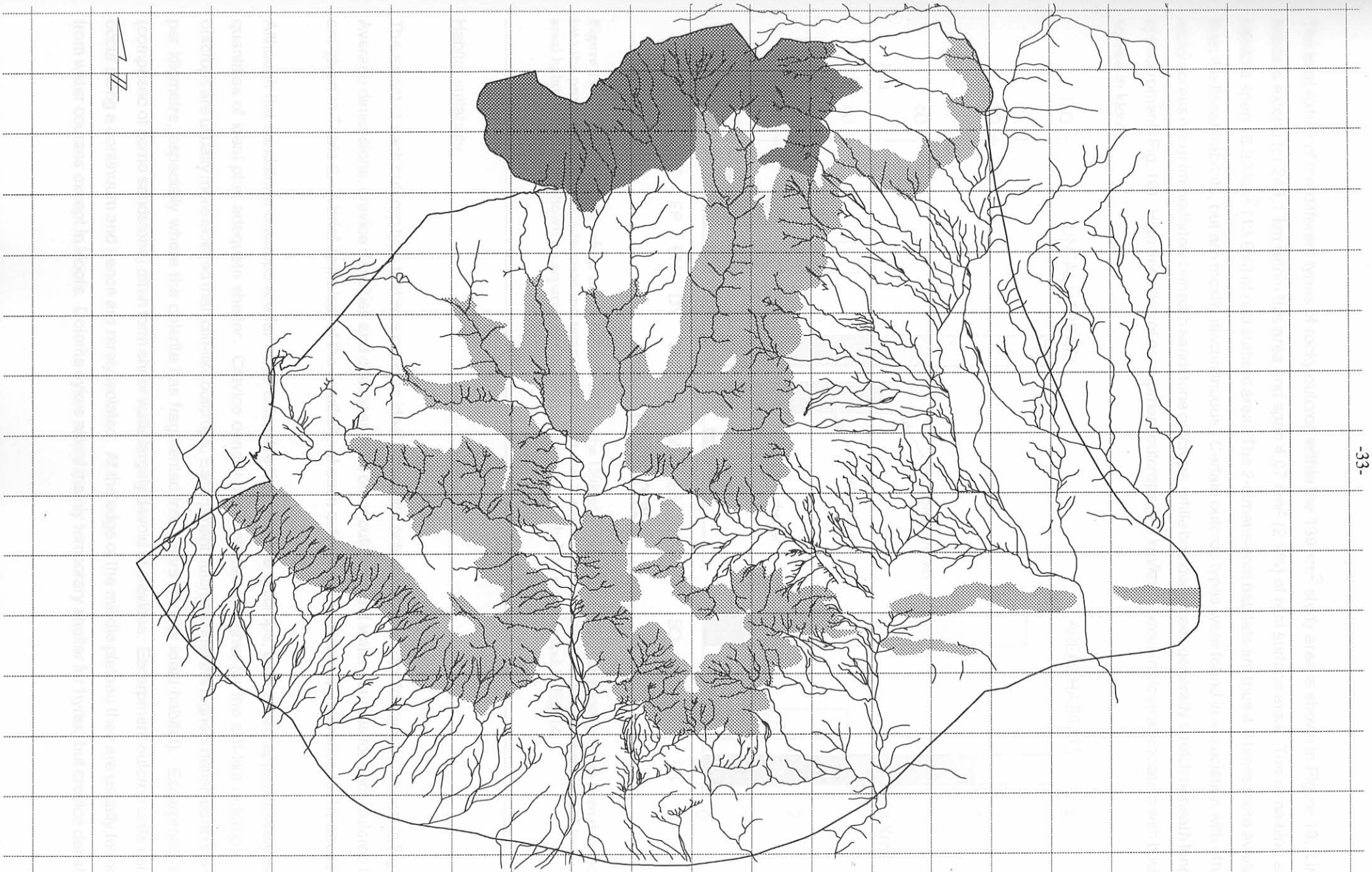




**Figure 17.** Routes of the episodic water courses in the Karoo National Park shown against the major topographical habitats within the mapped area (1km grid shown) generated from ARCINFO coverages using ARCVIEW

University of Pretoria etd – Davies, R A G (1994)



The total extent of the different types of rocky outcrop within the 139 km$^2$ study area is shown in Figure 19. Lineal habitats extend for 248.1 km within this area and span 4.07 km$^2$ (2.9%) of real surface area. The remaining areal habitats span 18.89 km$^2$ (13.6%) of real surface area. The 2-dimensional habitats are thus 4.6 times more available than the linear habitats, but are mostly discontinuous. Certain outcrop types were found in association with others: rocky screes occur immediately beneath sandstone outcrops, while boulder screes generally stretch beneath lengths of escarpment (Fig. 16). High densities of escarpment outcrops (4.9 km/km$^2$) occur in close association with boulder screes in kloofs.

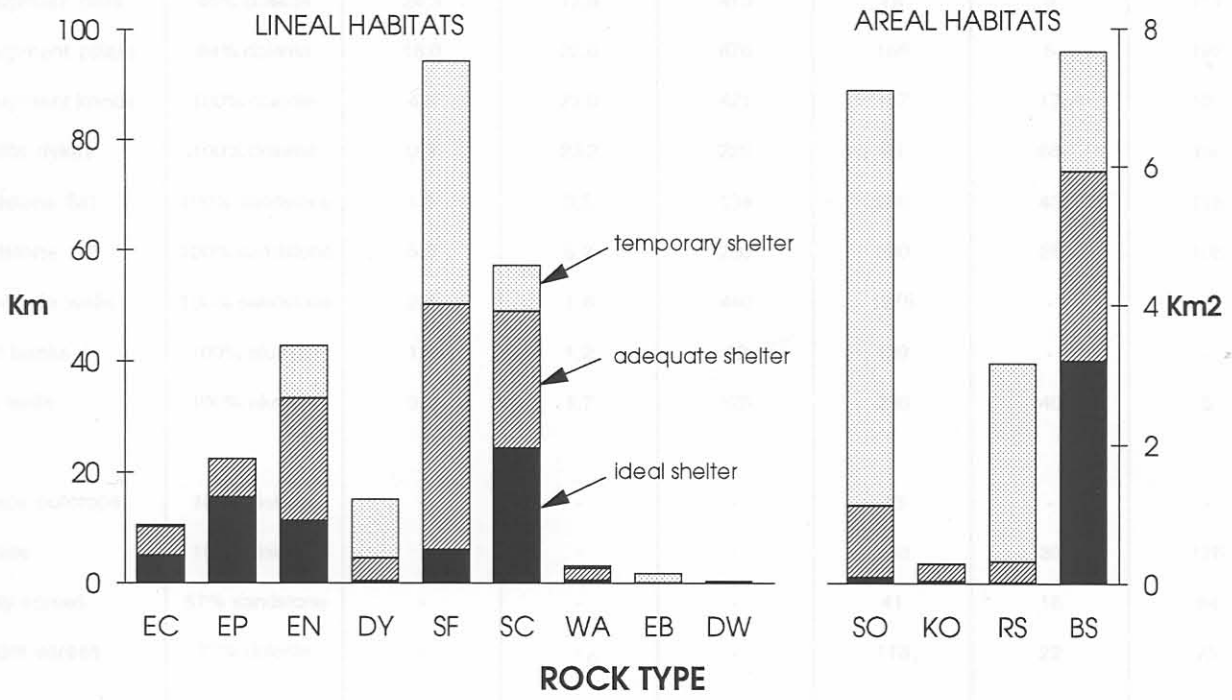



**Figure 19.** Total extent of refuge micro-habitats within the 139km$^2$ mapped area. Each outcrop type has been divided into the proportion of ideal, adequate and temporary shelter that it affords to rock hyrax (see habitat mapping). Lineal and areal habitats had to be shown on separate scales. For abbreviations of habitats, see legend in Fig. 14.

Habitat suitability

The extent of each outcrop type that was rated as ideal, adequate or temporary shelter for hyrax is shown in Fig. 19. Average dimensions, crevice densities and distances from other outcrops and water courses for each outcrop type are given in Table 2. A brief appraisal of the suitability of each outcrop type follows, in reference to the above.

Although flat sandstone outcrops are far more extensive than cliff-like outcrops, both afford approximately equal quantities of ideal plus adequate shelter. Crevice density per kilometre is higher for the cliff-like outcrops. Flat outcrops are usually more isolated than cliff-like outcrops. Escarpment outcrops offer the highest densities of crevices per kilometre, especially where the dolerite has fragmented into pillars (mostly ideal habitat). Escarpment cliffs (comprised of some sandstone) often form sheer walls largely devoid of crevices. Escarpment outcrop units usually occur along a continuum and hence are rarely isolated. At the edge of the middle plateau they are usually found far from water courses except in kloofs. Dolerite dykes afford mainly temporary shelter for hyrax, but crevice density is

University of Pretoria etd – Davies, R A G (1994)



TABLE 2

ATTRIBUTES OF THE PRINCIPAL REFUGE MICRO-HABITATS AVAILABLE TO ROCK HYRAX IN THE KAROO NATIONAL PARK

| ROCK TYPE | SUBSTRATE | mean height (m) | mean width (m) | CREVICE DENSITY No/km | CREVICE DENSITY No/ha | mean distance to outcrop (m) | mean distance to water course (m) |
|---|---|---|---|---|---|---|---|
| Escarpment cliffs | 46% dolerite | 24,3 | 17,8 | 413 | 78 | 9 | 111 |
| Escarpment pillars | 94% dolerite | 18,0 | 22,6 | 676 | 156 | 5 | 192 |
| Escarpment knobs | 100% dolerite | 4,3 | 21,0 | 421 | 187 | 17 | 100 |
| Dolerite dykes | 100% dolerite | 0,9 | 23,2 | 229 | 95 | 66 | 69 |
| Sandstone flat | 100% sandstone | 1,5 | 3,5 | 134 | 238 | 43 | 115 |
| Sandstone cliff | 100% sandstone | 5,3 | 5,2 | 230 | 200 | 25 | 106 |
| Man-made walls | 100% sandstone | 2,4 | 1,6 | 440 | 1275 | - | - |
| Earth banks | 100% aluvium | 1,9 | 1,2 | 42 | 139 | - | - |
| Dam walls | 100% aluvium | 3,0 | 1,7 | 125 | 286 | 40 | 5 |
| Surface outcrops | 100% dolerite | - | - | - | 46 | - | - |
| Koppies | 100% dolerite | - | - | - | 133 | 39 | 176 |
| Rocky screes | 57% sandstone | - | - | - | 41 | 16 | 84 |
| Boulder screes | 77% dolerite | - | - | - | 113 | 22 | 75 |

reasonable. Dykes are the only lineal habitats that stretch vertically down slopes, often running closely parallel to water courses, but usually far from other outcrops. Sandstone walls have exceptionally high densities of shallow crevices, providing mostly adequate shelter for hyrax. Earth banks have the lowest density of crevices, and only afford temporary shelter for hyrax. Earthen dam walls afford adequate shelter for hyrax colonies. Both earth banks and dam walls occur along water courses.

The dolerite surface outcrops and the predominantly sandstone rocky screes have very low densities of crevices per hectare and are made up of large areas of scattered rock suitable only as temporary shelter for hyrax. In the rocky screes, small rocks covered an estimated 48% of ground cover, large rocks (>0,7m) occurred at average densities of $27ha^{-1}$, and average density of boulders (>2m) was $0.4ha^{-1}$. Dolerite koppies provide similar crevice densities to escarpment outcrops, but afford mostly adequate shelter. Koppies are usually far from water courses and other outcrops. Crevices are far denser in boulder screes than rocky screes. Boulder screes contain an average of 57 large rocks $ha^{-1}$, 2.0 boulders $ha^{-1}$ and a ground cover of 25% small rocks. Many boulder screes contain very high densities of boulders, interspersed with impenetrable riparian thicket, thus affording an extensive ideal habitat, rich in food and shelter. Boulder screes and especially rocky screes occur in close association with other outcrops, and both tend to accumulate in depressions and along drainage routes (close to water courses).

University of Pretoria etd – Davies, R A G (1994)



Most adequate and ideal hyrax habitat is contained within escarpment, sandstone and boulder scree outcrops (Fig. 19), and one would expect these habitats (especially escarpment pillars and boulder screes) to accommodate most hyrax. Remaining outcrop types are either limited in extent (e.g. walls, koppies) or largely unsuitable for permanent colonies (e.g. dykes, surface outcrops, rocky screes). Crevice quality was not measured in this study but is speculated on in later chapters.

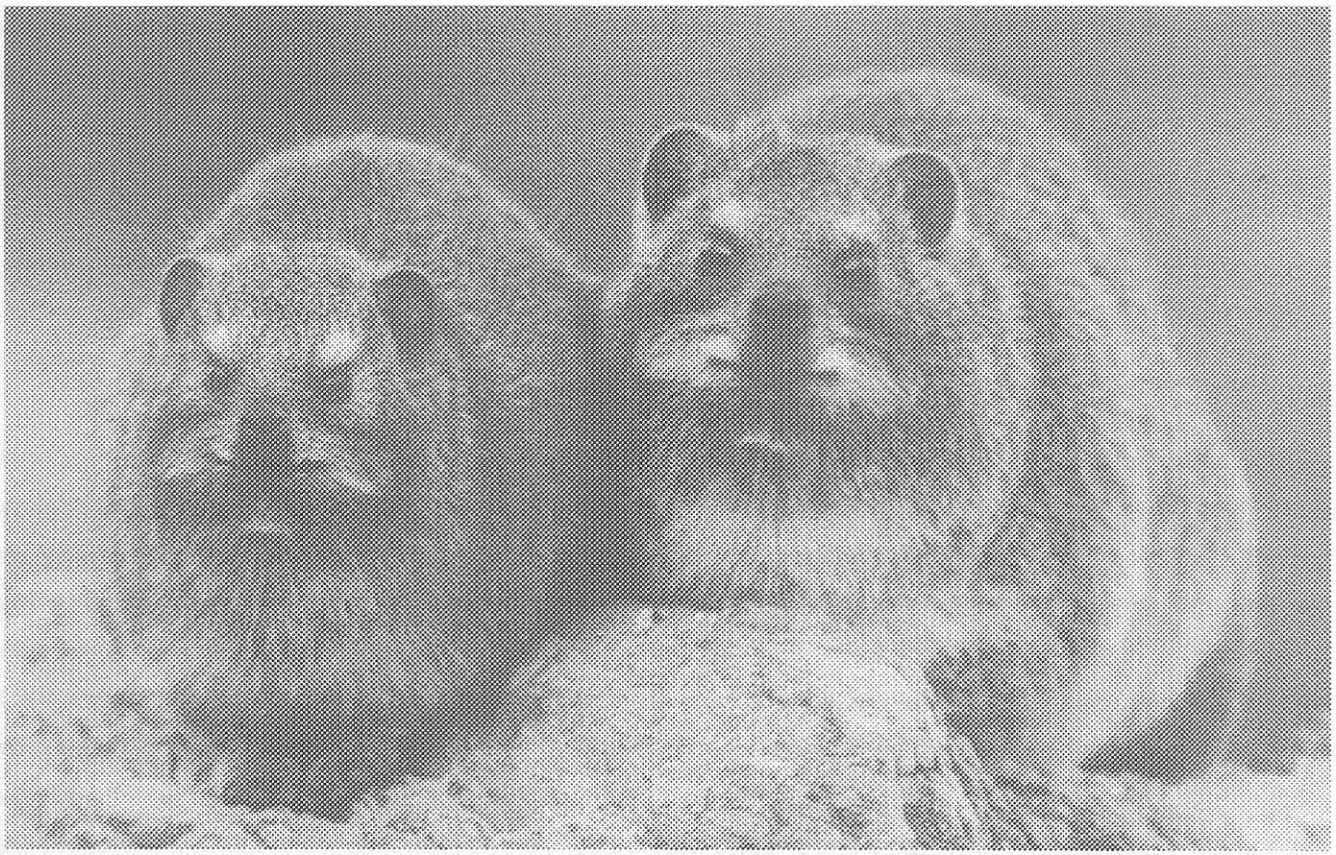
The refuge environment of rock hyrax in this study is different from that in most other studies so far. Rock hyrax are usually found in the igneous rock outcrops of Africa, particularly granite and its derivatives which may form large rounded domes with well scattered crevices as in the northern Cape (George & Crowther 1981), and in parts of the Matobo Hills (Gargett 1990), or isolated koppies which often comprise habitat islands in a sea of grassland as in the Serengeti (Turner & Watson 1965; Hoeck 1982) and parts of the Matobo Hills (Gargett 1990). Hyrax also inhabit boulder screes found along fault scarps and lateral glacial moraines in Kenya (Sale 1966) which are probably less isolated. The dolerites and sandstones of the eroded karoo landscape give rise to a patchy, but more contiguous network of escarpment and sandstone outcrops running across the slopes transected by dykes and screes running down the slopes. The substrates in the KRNP and MZNP are similar (see Fourie 1983) but this network of rocks appears to be more extensive and connected where the Great Escarpment is well-developed as at Beaufort West (pers. obs.). Another difference between this and other hyrax studies is that the short karoo shrubs in the KRNP afford less protection to hyrax than the dense vegetation found on rocky outcrops elsewhere in Africa. Of the major topographical habitats in the KRNP, clearly the mountain slopes should afford the best rocky network for safe feeding and dispersal by hyrax, but an irregular patchwork of surface outcrops should also permit some access to vegetation on the plateau habitats, while a few thin, long sandstone lenses should provide access to riparian thickets along river networks on the bottom plains. The variety of refuge habitats in the KRNP form an interactive mosaic of varying potential combinations of food and shelter, and this should be reflected in the distribution pattern of rock hyrax. One might anticipate that the interface between escarpment and boulder screes would provide the most suitable conditions for hyrax.



*Vigilant hyrax sunning in a favourite spot. Note the whitewash streaks on the rocks from $CaCO_3$ in hyrax urine.*

University of Pretoria etd – Davies, R A G (1994)

# *THE PREY BASE*



University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 4*

# *ROCK HYRAX DEMOGRAPHY AND BEHAVIOUR*

## INTRODUCTION

Rock hyrax are diurnal and social herbivores (weighing up to 4kg), and occur in the rocky habitats of Africa (Chapter 1). They are well able to cope with very arid regimes (Louw *et al.* 1972) such as the Karoo. Their association with rocky habitats has been described (see page 36) but seldom evaluated quantitatively. They are gregarious with a wide vocal repertoire (Fourie 1977). The social organisation of rock hyrax is common to many mammals (Clark 1978), where groups each consist of a matriline of up to 17 adult females monopolised by a single territorial male, with young of both sexes (Coe 1962; Hoeck, Klein & Hoeck 1982; Fourie & Perrin 1987b). Dispersal is usually more obligatory for immature male hyrax than immature females. However, this social organisation is known to be somewhat flexible (Hoeck *et al.* 1982). Rock hyrax can be prolific breeders and this aspect of their biology has attracted considerable scientific attention because of the agricultural importance of population irruptions (see page 2). In the Karoo, this breeding is distinctly seasonal (Millar 1971; Fourie 1983). *Procavia* species will graze and browse, but smaller species from the *Heterohyrax* genus (found further north in Africa) are predominantly browsers (Sale 1965; Turner & Watson 1965; Fourie 1983).

A thorough investigation of the influence of predation by black eagles and other predators on rock hyrax demography probably requires more knowledge of the prey base than of the predator guild. For the purposes of this study it was essential to obtain accurate estimates of hyrax population sizes in black eagle territories within the KRNP. The first part of this chapter outlines how this was done by close examination of the relationship between rock hyrax and their refuge resources which were described in the last chapter. Two methods of population estimation are considered. Knowledge of the distribution patterns of hyrax within these habitats and their behaviour was also needed to interpret black eagle foraging behaviour in Chapter 6. Presentation of behavioural data in this chapter is mainly limited to behaviour which is relevant to the hyrax population model evolved in Chapter 12, but I take the opportunity to describe anti-predator behaviour and to speculate on the origins of rock-dwelling and group-dwelling behaviour in this species. Prey defence behaviour is often over-looked in predator-prey studies (Malcom 1992). Besides abundance of rock hyrax, it was necessary to gain a comprehensive understanding of the structure and processes of this prey population. This chapter considers factors other than predation, particularly climate, which may cause or influence the loss or addition of individuals to the hyrax population.

University of Pretoria etd – Davies, R A G (1994)



## METHODS

*Annual censuses at hyrax colonies*

Rock hyrax are known to be thermally labile and must raise their body temperature each morning before feeding, usually by sunbathing (page 26). This affords the best opportunity of getting an accurate total count of a particular group. Most hyrax groups consistently overnight in certain outcrops but some move between locations (see later). I use the term group when referring to the social unit and colony when referring to a regularly-used outcrop.

I counted hyrax groups from distances ranging from 50-150m using a pair of Swift Satellite 20*80 binoculars mounted on a tripod. Before the sun reached the colony, I positioned myself with an unobstructed view of its east-facing aspect and remained there for approximately 90 min. or until I had obtained a satisfactory count. I made regular sweeps of the study group until I obtained a consistent tally for each of three identifiable age classes (Figure 20). At first, the hyrax line up side by side immediately outside their crevices allowing close comparison of body size.

Initial doubts about the accuracy of these counts were largely dispelled by conducting sample counts immediately prior to intensive behavioural observations (see later) of specific groups. Confident estimates of group size are obtained during such detailed observations, and the sample counts were in close agreement with these. However the counts did prove to be weather-dependent. On cold, still, sunny mornings hyrax sit on top of rocks and an accurate count can be obtained within 30 min. of the sun reaching the colony. But hyrax sunbathe in sheltered (concealed) nooks in windy conditions; their sunbathing is brief on warm mornings and may not be synchronised; and their emergence

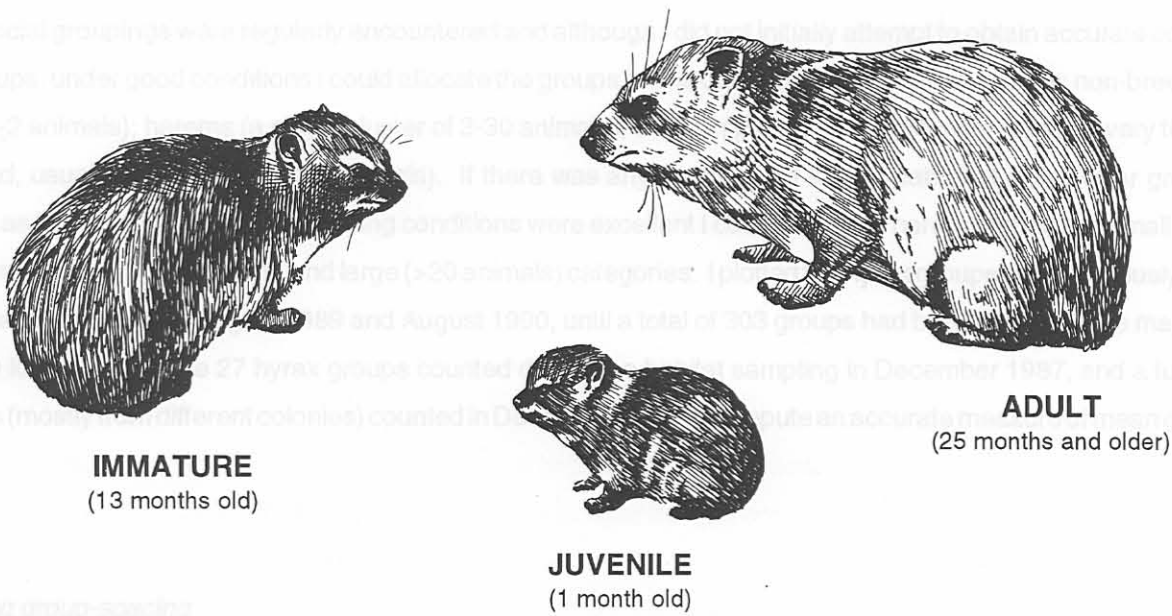



**Figure 20.** The three age classes discernible during counts conducted during December (@ one month after the birth-pulse) in the KRNP: juveniles (average mass 0,25kg) are easily told by their small size; immatures (average mass 1,65kg) usually have a darker grey pelage than adults with bolder facial markings, they also have shorter noses and more pronounced foreheads; the eyes of adults are situated midway between nose and ears, whereas on immatures the eyes are situated closer to the nose. Adults weigh approximately 3,2kg.

University of Pretoria etd – Davies, R A G (1994)



is asynchronised and occurs much later in the day on cold, overcast mornings; they can remain in their crevices for two to three days when conditions are cold and wet (Coe 1962; pers. obs.). As a result of these influences I often had to repeat counts up to four times until I was satisfied with the result.

Rock hyrax in the Karoo show a distinct birth-pulse. Fourie (1983) noted that 92% of hyrax births in the MZNP (Fig. 3, page 8) occurred within four weeks (November to December) of the first birth for that season. In the Noorsveld (Fig. 3) 81% of hyrax births occurred in November (Millar 1971). Modal parturition date in this study was 12 November (see later) with the first babies appearing at the end of October. I began counts 18d after the modal parturition date so that at least 90% of females should have given birth by the start of the counts. Counts extended through the month of December and were conducted annually at sixteen colonies in the KRNP in 1987, 1988, 1989 and 1990 to assess recruitment, population composition and relative abundance.

*Estimating hyrax density*

Initial estimates of hyrax density from total counts of habitat strips (27 groups in 90 stretches of rock outcrop) conducted in December 1987 using Caughley's formula for unequal-sized sampling units in stratified habitats (Caughley 1977) proved unrealistic (discussion). But these counts did indicate notable consistency of group size and subsequent effort was directed at plotting all hyrax groups in the study area and accurately determining mean group size. I plotted all hyrax groups on a given slope by climbing to a commanding viewpoint (within about one kilometre range) at dawn and scanning the rock outcrops on the slope as the sun reached them. Weather affected this technique in the same way as it affected the regular counts. I used the same equipment for both methods.

Certain social groupings were regularly encountered and although I did not initially attempt to obtain accurate counts of the groups, under good conditions I could allocate the groups to one of three loose social categories: non-breeding groups (1-2 animals); harems (a single cluster of 3-30 animals); and complexes (2-4 clusters of animals, very tightly associated, usually totalling 30-45 individuals). If there was any doubt about the allocation of a particular group I classed it as 'undetermined'. When viewing conditions were excellent I could separate harem groups into small (<12 animals), medium (12-20 animals) and large (>20 animals) categories. I plotted the hyrax groups simultaneously with habitat-mapping between August 1989 and August 1990, until a total of 303 groups had been plotted in the mapped area (139 $km^2$). I used the 27 hyrax groups counted during the habitat sampling in December 1987, and a further 27 groups (mostly from different colonies) counted in December 1989 to compute an accurate measure of mean group size.

*Measuring group-spacing*

Nearest neighbour distances between groups were used in computation of the G-statistic (Brown 1975; Brown & Rothery 1978). This index has been shown to give a robust indication of dispersion pattern (Watson & Rothery 1986), and can detect regular-spacing on a small scale irrespective of larger-scale pattern. It is obtained from the ratio of

University of Pretoria etd – Davies, R A G (1994)


the geometric mean to the arithmetic mean of the squared nearest neighbour distances. The index scales between 0 and 1 where high values indicate regularity and values less than about 0,65 indicate randomness (Nilsson, Nilsson & Slyven 1982).

*Destructive sampling*

Hyrax were shot during October 1989 (n=26) and October 1990 (n=26), just prior to the birth pulses, to check recruitment as determined from the counts against fecundity. The shot sample also provided information on age structure, sex ratio and body masses of the hyrax. On account of low hyrax density, destructive sampling proved time-consuming and had to be restricted so as not to interfere with other work. Weight, age, sex and reproductive details were recorded for each animal shot. Patterns of tooth eruption and tooth wear (on the maxillae) were used to determine the age of the animals (see the methods section in Chapter 10). The age distribution of 53 hyrax skulls, that were picked up in the study area (most during 1987), was determined in the same way in order to construct mortality schedules. These skulls were collected away from known predator feeding sites in order to avoid any selective bias by predators.

*Behavioural observations*

Chosen hyrax groups were observed in periods of five consecutive days from dawn to dusk. I tried the method of Fourie & Perrin (1986) to trap individuals in one group but abandoned this effort after no success was achieved in a two-week period. I was able to use behavioural cues to identify territorial males and other social classes in some instances. Every fifteen minutes the following parameters were recorded for each visible individual hyrax onto maps of the colony or onto a database: age (as for counts), activity, location, distance from nearest shelter, distance from overnighting outcrop, whether the animal was in the sun or the shade, whether the animal was huddling with other hyrax, and whether the animal was vigilant or performing sentinel behaviour. Meteorological conditions and the presence or absence of predators were noted at each 15min observation.

*Vegetation analyses*

Apparent 'vegetation zones' around hyrax colonies were investigated in the following manner. Four 30m transect lines were laid out radiating north, east, south and west from an isolated boulder colony. Every metre along these transects a quadrat (1m square) was laid alongside the transect line, and the following parameters were recorded within it: an ocular estimate of the proportion of the quadrat comprised by bare rock; the number of hyrax faeces; the number of ungulate faeces; distance to nearest large rock (shelter); distance to nearest tall shrub (shelter); and for each plant species identified within the quadrat - the name, number of plants, an ocular estimate of the proportion of the quadrat comprised by the canopy spread of that species, an ocular estimate of the proportional leaf cover within that canopy spread, and an ocular estimate of the proportion of shoots cropped on that species.

University of Pretoria etd – Davies, R A G (1994)



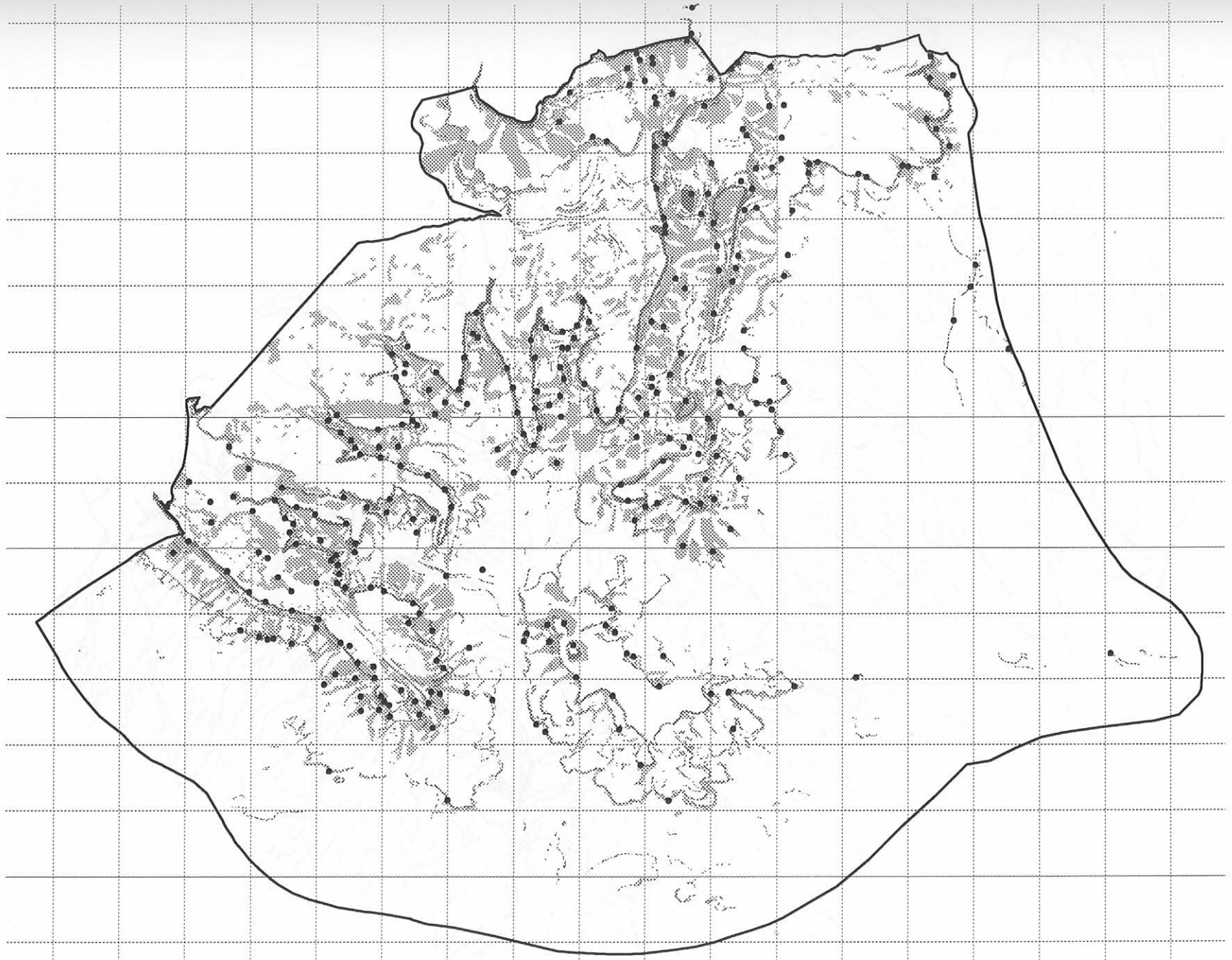


**Figure 21.** Distribution of hyrax groups (n=303) in relation to the refuge micro-habitats of the KRNP. Consult Fig. 16 for details on refuge micro-habitats. Upper slopes below 'toerenjies' (protrusion in top left corner) were not completely surveyed for hyrax groups. 1km grid and boundary of mapped area shown. Generated from ARCINFO coverages using ARCVIEW

University of Pretoria etd – Davies, R A G (1994)

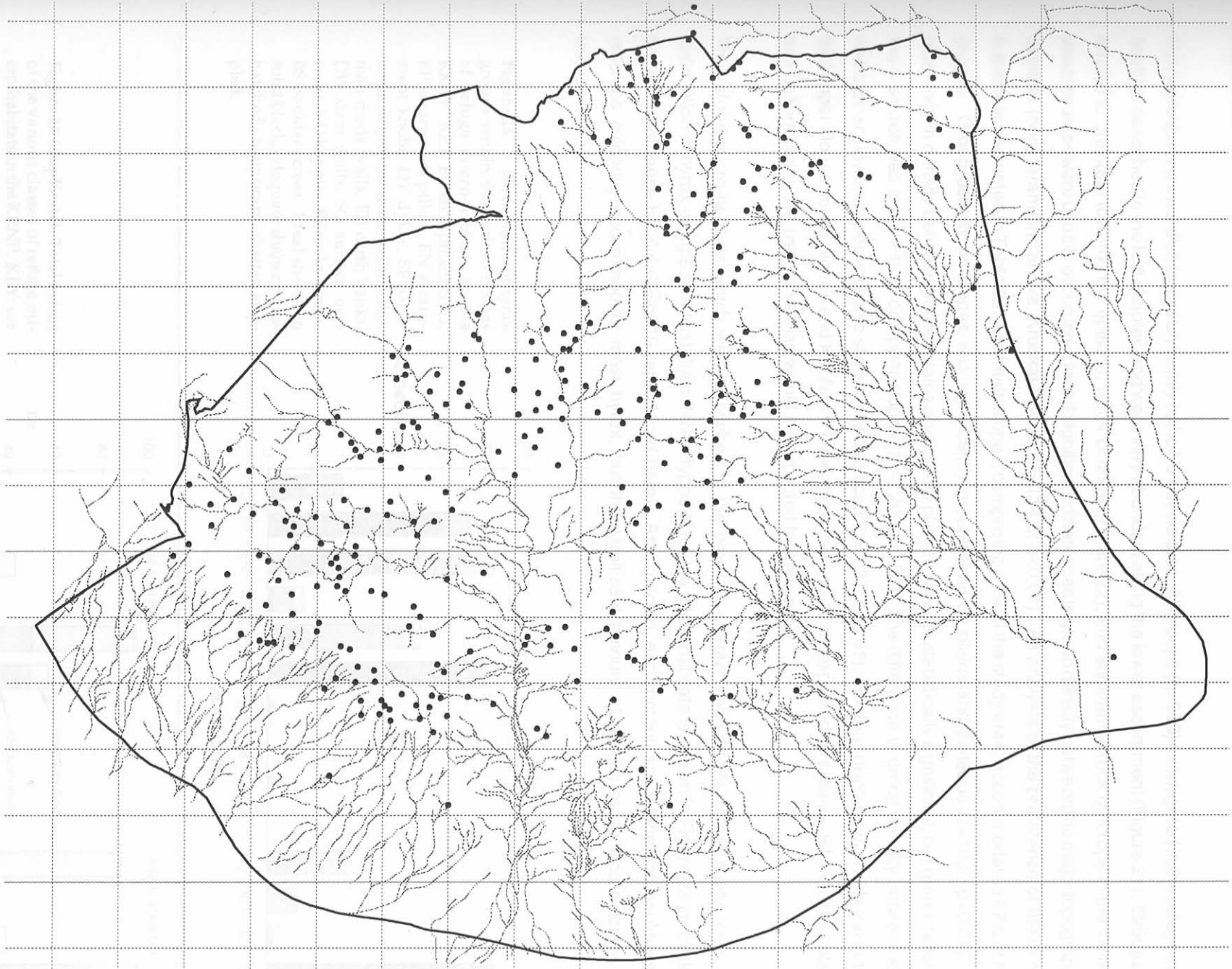


**Figure 22.** Distribution of hyrax groups (n=303) in relation to the episodic water courses of the KRNP (1km grid and boundary of mapped area shown) (generated from ARCINFO coverages using ARCVIEW)

University of Pretoria etd – Davies, R A G (1994)



RESULTS (cont.)

*Habitat use*

Hyrax groups were not distributed uniformly in the Nuweveld area. All groups (n=303) overnighted in the refuge micro-habitats described in the last chapter, and were very abundant along the lower escarpment (Figure 21). Groups also tended to gravitate towards the episodic water courses (Figure 22), and substantial rock outcrops in the vicinity of water courses were usually occupied. I found significant differences in group density between the major topographical habitats (non-parametric anova, Kruskal-Wallis: $X^2$=114,5; p<0,01). An analysis of the preference of these major habitats is presented in Table 3a. Mountain slopes, comprising 31% of the study area, accommodated 87% of hyrax groups. Group density on slopes was significantly greater than on plains and plateaus (z=10,2; p<0,01). The difference in density between bottom plains and middle plateau was not statistically significant, but group density on lower slopes was greater than on upper slopes (z=-2,20; p<0,05). The difference in group density between kloofs and ordinary lower slopes was also statistically significant (z=4,27; p<0,01). Bonferroni intervals (Table 3a) indicate that upper slopes, lower slopes and kloofs are used more than would be expected by chance, while middle plateau and bottom plains are used less than would be expected by chance.

The refuge micro-habitats which were described in the previous chapter span 16,5% of the study area. The distribution of hyrax groups amongst the different types of refuge micro-habitats is shown in Figure 23 in relation to the extent of these habitats (Fig. 19 reproduced here). As expected, escarpment, sandstone and boulder scree outcrops evidently accommodate most hyrax, but the significant amount of groups in surface outcrops was unexpected.

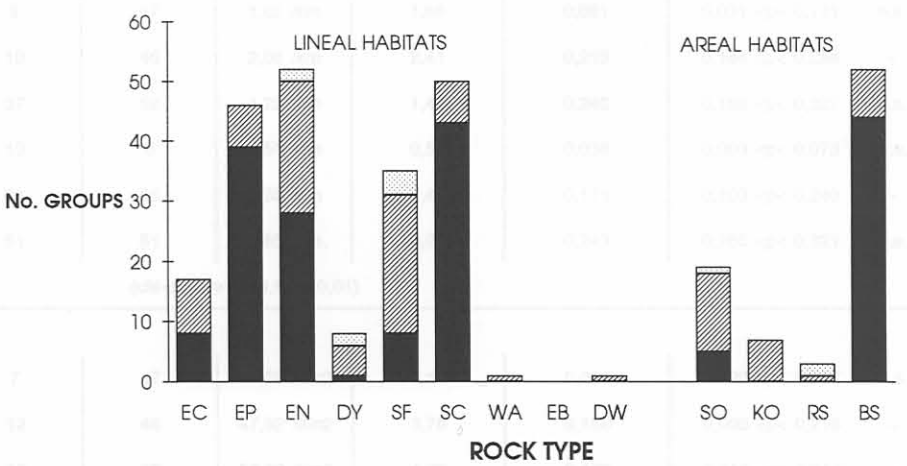



**Figure 23.** Distribution of hyrax groups within the various classes of refuge micro-habitats in the KRNP. KEY: EC escarpment cliffs, EP escarpment pillars, EN escarpment knobs, DY dykes, SF sandstone flat, SC sandstone cliffs, WA man-made walls, EB earth banks, DW dam walls, SO surface outcrops, KO koppies, RS rocky screes, BS boulder screes. Ideal shelter in solid black, adequate shelter cross-hatched, temporary shelter stippled.

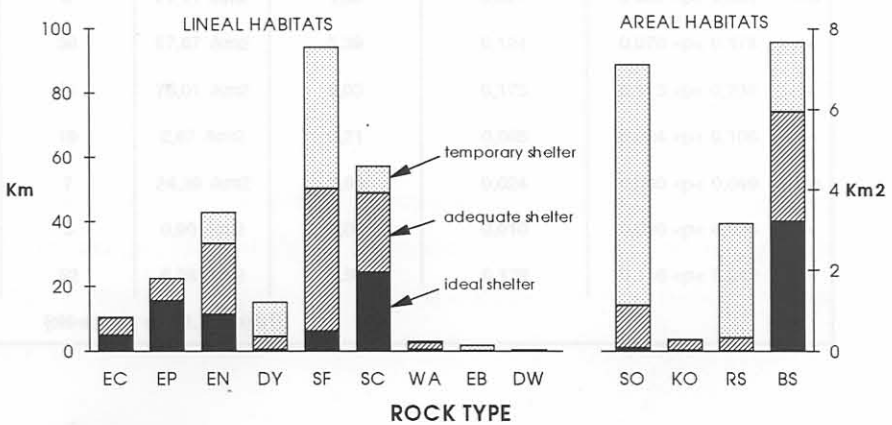



**Figure 19 (duplicate).** Total extent of the various classes of refuge micro-habitats in the KRNP. KEY: see above.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 3
## ANALYSIS OF HYRAX HABITAT PREFERENCES

Observed and expected frequencies of hyrax groups in different habitats are compared using the Chi-square statistic which is presented beneath each analysis. A simple preference rating is provided for each habitat type by dividing proportionate use by proportionate availability, after Petrides (1975). Bonferroni confidence intervals on the expected proportional use of each habitat were calculated as described by Neu, Byers & Peek (1974) and Byers, Steinhorst & Krausman (1984). If the observed proportional use of any habitat falls outside of these intervals it demonstrates a statistically significant preference for (+) or against (-) that habitat.

| HABITAT | EXTENT | EXPECTED NO. GROUPS | OBSERVED NO. GROUPS | GROUP DENSITY | PREFERENCE RATING | OBSERVED PROPORTIONAL USE | 95% BONFERRONI CONFIDENCE INTERVALS | |
|---|---|---|---|---|---|---|---|---|
| A. preference of the major topographical habitats: | | | | | | | | |
| UPPER SLOPES | 4,86 km2 | 10 | 25 | 5,14 /km2 | 2,46 | 0,086 | 0,044 <p< 0,128 | + |
| MIDDLE PLATEAU | 25,60 km2 | 54 | 25 | 0,98 /km2 | 0,47 | 0,086 | 0,044 <p< 0,128 | - |
| LOWER SLOPES | 34,13 km2 | 72 | 176 | 5,16 /km2 | 2,46 | 0,605 | 0,531 <p< 0,679 | + |
| KLOOFS | 4,00 km2 | 8 | 51 | 12,76 /km2 | 6,03 | 0,175 | 0,118 <p< 0,232 | + |
| BOTTOM PLAINS | 70,24 km2 | 147 | 14 | 0,20 /km2 | 0,10 | 0,048 | 0,016 <p< 0,080 | - |
| (chi-square = 539,7; p<0,01) | | | | | | | | |
| B. preference of lineal vs. areal refuge micro-habitats | | | | | | | | |
| LINEAL | 4,07 km2 | 52 | 210 | 51,58 /km2 | 4,08 | 0,722 | 0,663 <p< 0,781 | + |
| AREAL | 18,89 km2 | 239 | 81 | 4,29 /km2 | 0,34 | 0,278 | 0,219 <p< 0,337 | - |
| (chi-square = 589,0; p<0,01) | | | | | | | | |
| C. preference of lineal refuge micro-habitats by length | | | | | | | | |
| ESCARPMENT CLIFFS | 10,49 km | 9 | 17 | 1,62 /km | 1,88 | 0,081 | 0,031 <p< 0,131 | n.s. |
| ESCARPMENT PILLARS | 22,38 km | 19 | 46 | 2,06 /km | 2,41 | 0,219 | 0,144 <p< 0,294 | + |
| ESCARPMENT KNOBS | 42,80 km | 37 | 52 | 1,22 /km | 1,43 | 0,248 | 0,169 <p< 0,327 | n.s. |
| DYKES | 15,67 km | 13 | 8 | 0,51 /km | 0,59 | 0,038 | 0,003 <p< 0,073 | n.s. |
| SANDSTONE (FLAT) | 94,67 km | 81 | 36 | 0,38 /km | 0,45 | 0,171 | 0,103 <p< 0,240 | - |
| SANDSTONE (CLIFFS) | 60,28 km | 51 | 51 | 0,85 /km | 0,99 | 0,243 | 0,165 <p< 0,321 | n.s. |
| (chi-square = 78,5; p<0,01) | | | | | | | | |
| D. preference of all refuge micro-habitats by area | | | | | | | | |
| ESCARPMENT CLIFFS | 0,56 km2 | 7 | 17 | 30,58 /km2 | 2,42 | 0,058 | 0,020 <p< 0,097 | n.s. |
| ESCARPMENT PILLARS | 0,97 km2 | 12 | 46 | 47,52 /km2 | 3,76 | 0,158 | 0,098 <p< 0,218 | + |
| ESCARPMENT KNOBS | 0,97 km2 | 12 | 52 | 53,89 /km2 | 4,26 | 0,179 | 0,116 <p< 0,242 | + |
| DYKES | 0,38 km2 | 5 | 8 | 21,11 /km2 | 1,59 | 0,027 | 0,000 <p< 0,054 | n.s. |
| SANDSTONE (FLAT) | 0,53 km2 | 7 | 36 | 67,67 /km2 | 5,39 | 0,124 | 0,070 <p< 0,178 | + |
| SANDSTONE (CLIFFS) | 0,67 km2 | 8 | 51 | 76,01 /km2 | 6,03 | 0,175 | 0,113 <p< 0,238 | + |
| SURFACE OUTCROPS | 7,11 km2 | 90 | 19 | 2,67 /km2 | 0,21 | 0,065 | 0,024 <p< 0,106 | - |
| KOPPIES | 0,29 km2 | 4 | 7 | 24,39 /km2 | 1,85 | 0,024 | 0,000 <p< 0,049 | n.s. |
| ROCKY SCREES | 3,33 km2 | 42 | 3 | 0,90 /km2 | 0,07 | 0,010 | 0,000 <p< 0,026 | - |
| BOULDER SCREES | 8,16 km2 | 103 | 52 | 6,38 /km2 | 0,50 | 0,179 | 0,116 <p< 0,242 | - |
| (chi-square = 586,7; p<0,01) | | | | | | | | |

University of Pretoria etd – Davies, R A G (1994)



Hyrax evidently highly prefer lineal habitats and avoid areal habitats in terms of density per square kilometre (Table 3b), these trends cannot be attributed to chance. Hyrax groups in lineal habitats occur at 12 times the density of those in areal habitats.

Within the preferred lineal habitats differences also occur between their use and availability (Table 3c). All escarpment outcrop types are used in greater proportion than their availability by length but only in the case of escarpment pillars is this preference statistically significant. Flat sandstone outcrops are significantly avoided; dykes also appear to be under-utilised; while cliff-like sandstone outcrops are used in proportion to their availability. No groups were observed in earth banks. Walls and dam walls were too limited to include in this analysis, but two artificial rock structures constructed in the study area were rapidly colonised by hyrax groups.

If one considers all outcrop types in terms of their area this pattern is changed (Table 3d): all lineal habitats now appear to be used in greater proportion than their availability (as was indicated in Table 3b); in the case of escarpment pillars and knobs, and sandstone outcrops this preference is statistically significant; but in this treatment the narrower outcrop types (escarpment knobs, sandstone outcrops) now appear to be the most preferred.

Of the areal habitats in Table 3d, only koppies are used in greater proportion than their availability but this preference is not statistically significant. Surface outcrops and both types of scree (especially rocky screes) are actually avoided by hyrax, and this cannot be attributed to chance. Ideal boulder screes are only used roughly in proportion to their availability (preference rating 1,02).

The distribution of whitewash streaks indicated heavier use of cliff-like sandstone outcrops, koppies and some escarpment outcrops than did the present distribution of hyrax groups. But the relationship between density of hyrax groups and density of whitewash streaks in the Kortkloof subsample of outcrops was strong ($r=0,836$; $p<0,01$). Outcrops harbouring hyrax in the Kortkloof subsample were surrounded by more tall shrubs than outcrops without hyrax (Kruskal-Wallis H test; $p<0,05$).

*Factors influencing use of slopes*

The use of slopes (n=296; see Fig. 15, page 29) by hyrax groups was predictably influenced by the distribution of preferred outcrop types. As expected, hyrax density was high on slopes where the density of outcrop units was high ($r=0,77$; $p<0,01$) and where the density of rock crevices was high ($r=0,74$; $p<0,01$).

Hyrax density showed stronger correlations with the density of lineal habitats ($r=0,81$; $p<0,01$) than with the density of areal habitats ($r=0,58$; $p<0,01$). The strongest relationships were observed with densities of favourite outcrop types (e.g. escarpment pillars: $r=0,72$; $p<0,01$). The density of all escarpment outcrops, except those rated as temporary shelter, was the best single indicator of hyrax density ($r=0,86$; $p<0,01$). This measure alone explained nearly three quarters of the total variation in hyrax density. Weakest or negative relationships were observed between hyrax density and unpreferred habitats such as dykes ($r=-0,10$; $p>0,10$) and surface outcrops ($r=-0,24$; $p<0,05$).

University of Pretoria etd – Davies, R A G (1994)



A regression model ($R^2$ option in the SAS computer programme, see Ingraham *et al.* 1988) incorporating escarpment outcrops, sandstone outcrops and koppies (all temporary shelter excluded) explained 83% of the variation in group density. The inclusion of parameters describing the density of screes had negligible influence on the predictive value of this model. The density of large rocks on a given slope showed a closer relationship with hyrax density (r=0,62; p<0,01) than did the density of rocky screes (r=0,48; p<0,01) or boulder screes (r=0,55; p<0,01).

The relationship between group density and the density of lineal habitats (r=0,78; p<0,01) was improved when outcrops providing only temporary shelter were excluded (r=0,81; p<0,01), but was weakened again if only ideal outcrops were considered (r=0,68; p<0,01). The same trend was even more apparent for areal habitats, and held for most outcrop types treated individually.

With regard to aspect, there was no significant difference in group density between north- (7,84km$^{-2}$) and south- (7,72km$^{-2}$) facing slopes, but there were significantly more groups on east- (8,94km$^{-2}$) than west- (5,92km$^{-2}$) facing slopes if a one-tailed test could be justified (Kruskal-Wallis H test: z=-1,75; p<0,05).

*Group size*

Mean group size at the end of 1987 was 17,4 (n=26; s.d.=12,2), while at the end of 1989 it was 16,4 (n=25; s.d.=10,3). Non-breeding groups (mean group size=1,25; s.d.=0,5; n=8) and complexes (mean group size=32,2; s.d.=8,2; n=10) accounted for much of the high degree of variation in these samples and their relative contribution is able to profoundly influence the overall mean. Mean group size of harems was 16,4 (s.d.=7,3; n=17) at the end of 1987, and 16,4 (s.d.=5,8; n=16) again at the end of 1989. Harems comprised 82,3% of groups plotted, non-breeding groups 9,2%, and complexes 8,5%. Using these frequencies (based on the more extensive group-plotting exercise) with the relevant group sizes given above yields an overall group size of 16,2 (close to that for harems), and indicates that 82,6% of hyrax occur in harem groups, 15,8% in complexes and 0,7% in non-breeding groups.

Harems and complexes are not likely to have been missed by this group plotting method. But relatively more non-breeding groups (15,7% of sample) were observed during the more thorough total counts of habitat strips at the end of 1987. It is quite likely that some non-breeding groups were over-looked by the group plotting method. If non-breeding groups do comprise 15,7% of groups in the real population then the number of groups plotted should be increased by 7,75% to compensate for those missed and real mean group size probably approaches 15,3. Total population estimates with this compensation are 1,24% greater than estimates without.

*Influence of habitat on group size*

Within the sample of 53 hyrax groups counted at the end of 1987 and 1989, larger groups were associated with rock outcrops of lower (more ideal) suitability ratings (r=-0,30; p<0,05). The same trend was evident from the distribution of groups categorised during the group plotting exercise: 87% of complexes and 71% of medium/large harems

University of Pretoria etd – Davies, R A G (1994)



occurred in ideal habitat; whereas only 43% of non-breeding groups and 38% of small harems occurred in ideal habitat. Some small harems were observed inhabiting temporary shelter.

I used a $X^2$ contingency table to investigate associations between the different social categories and particular rocky habitats. Certain categories were aggregated to allow calculation of adequate expected frequencies. Only two out of fifteen cells had expected frequencies less than five (viz. 4,56 and 4,80). I found a statistically significant association between certain social groupings and particular outcrop classes ($X^2$=17,3; p<0,05). Scrutiny of the contingency table revealed positive associations between large groups (large harems and especially complexes) and boulder screes; between medium harems and escarpment pillars or cliffs; and between small groups (non-breeders and small harems) and marginal habitats (flat sandstone outcrops, dykes, surface outcrops and rocky screes). Negative associations occurred between large groups and marginal habitats; and between small groups and escarpment cliffs or pillars. Remaining habitat types (escarpment knobs, koppies and sandstone cliffs) showed no obvious associations with any social grouping. Generally speaking, large groups and medium harems occupied the preferred habitats (as indicated by group density), while small groups were found in unpopular habitats.

Certain social groupings were also associated with habitats where an interaction of outcrop types occurred. Complexes occurred at greater frequencies than expected (and non-breeding groups at lower frequencies than expected) in kloofs where high densities of escarpment outcrops coincide with boulder screes, when compared with ordinary lower slope habitats ($X^2$=7,93; p<0,05).

*Group spacing*

Mean nearest neighbour distance amongst 291 plotted groups (Fig. 21) was 0,241km (s.d.=0,112), or when groups on the plains and plateaus were excluded 0,238km (s.d.=0,111; n=248). The nearest neighbour distances in this study yielded a value of 0,66 for the G-statistic, this indicates a dispersion pattern that is borderline between a regular and random distribution.

*Population estimates, density and biomass*

A total of 291 hyrax groups were plotted within the 136km$^2$ study area (flat surface area). At a mean group size of 16,23 hyrax, this yields a population estimate of 4723 hyrax in the study area. Compensation for overlooked non-breeding groups (see group size) increases this estimate to 4782 hyrax. The population estimate derived from the earlier method (total counts in habitat strips) was 30% greater than this.

Hyrax occur at a density of 35,2km$^{-2}$ in the study area. Density was 69,2km$^{-2}$ in the mountainous terrain (bottom plains excluded), or 103,0km$^{-2}$ on the slopes (plains and plateaus excluded). Hyrax densities in the major topographical habitats are used with the extent of these habitats to extrapolate a population estimate for the Karoo National Park in Table 4. All density estimates represent hyrax numbers just after the birth-pulse at the end of 1989.

University of Pretoria etd – Davies, R A G (1994)



At this time of the year the population is swamped with juveniles, and mean hyrax mass is only 1650g (the calculation of this figure is described later). This figure of mean mass was used to determine biomass in the various habitats (Table 4). Overall biomass in the mountainous terrain was 1,14kgha$^{-1}$. The kloof habitat had the highest values of density (221,7km$^{-2}$) and biomass (3,66kgha$^{-1}$).

TABLE 4

DENSITY AND BIOMASS OF ROCK HYRAX IN THE MAJOR TOPOGRAPHICAL HABITATS AND A POPULATION ESTIMATE FOR THE KAROO NATIONAL PARK

All data refer to hyrax numbers just after the birth-pulse (in December 1989). Hyrax densities are derived from the group densities given in Table 3 and include compensation for non-breeding groups that may have been overlooked by the group-plotting method. Density estimate for the upper plateau is taken from that of the middle plateau - a topographically similar habitat. Surface areas of slopes are two-dimesnional (no compensation for gradient). The extent of the park in this analysis is as described in Chapter 2.

| HABITAT STRATUM | EXTENT (km2) | DENSITY (No./km2) | BIOMASS (kg/ha) | No. HYRAX |
|---|---|---|---|---|
| UPPER PLATEAU | 33,83 | (16,0) | (0,26) | 541,3 |
| UPPER SLOPES | 38,40 | 92,7 | 1,53 | 3559,7 |
| MIDDLE PLATEAU | 62,27 | 16,0 | 0,26 | 996,3 |
| LOWER SLOPES & KLOOFS | 75,86 | 103,5 | 1,71 | 7851,5 |
| BOTTOM PLAINS | 117,14 | 3,3 | 0,05 | 386,6 |
| | | | TOTAL IN PARK : | 13335 |

*Population composition*

A modal conception date of 27 March and a modal parturition date of 12 November were calculated from the masses of litters from pregnant females shot during October (see Fourie 1983 for method). A total of 89 counts at hyrax localities revealed that immediately after the hyrax birth pulses of 1987, 1988, 1989 and 1990, overall population composition was 35,3% juveniles (one month old); 18,1% immatures (13 months old); and 46,5% adults (25 months and older).

Three of the eighteen hyrax colonies regularly-counted disappeared during this study through emigration or mortality. A complete coverage for all years was obtained for only twelve localities. Comparisons between years are based on these 12 localities. A summary of the counts made at these localities is given in Table 5.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 5
## RESULTS OF THE ANNUAL HYRAX COUNTS

The first four columns summarise annual counts made during December at twelve regular localities. The last column summarises data from all the counts (n=89) at all localities. Percentages are given in brackets. Only groups that remained extant throughout the study period were considered for the comparison of group size. Age and sex classes were separated on the assumptions described in the methods section: adults in tight groups were considered to consist of one territorial male and the remainder females; solitary adults which were loosely associated with groups were taken to be peripheral males. Mortality was determined for the two categories by comparing numbers of that category in one year with numbers of the appropriate category the following year. Annual rainfall (January to December) and rainfall for the three months prior to the birth-pulse are given in mm.

| | END '87 | END '88 | END '89 | END '90 | OVERALL |
|---|---|---|---|---|---|
| TOTAL COUNT | 252 | 185 | 211 | 188 | 1328 |
| No. HAREMS | 15 | 14 | 13 | 13 | 84 |
| MEAN GROUP SIZE | 22,8 | 16,6 | 19,2 | 18,4 | |
| ADULTS | 120 (48) | 84 (45) | 92 (44) | 94 (50) | 617 (46,5) |
| IMMATURES | 43 (17) | 29 (16) | 30 (14) | 53 (28) | 241 (18,1) |
| JUVENILES | 89 (35) | 72 (39) | 88 (42) | 41 (22) | 469 (35,3) |
| JUVENILE MORTALITY | 60 (67) | 42 (58) | 35 (40) | | (55,2 p.a.) |
| ADULT & IMMA. MORTALITY | 79 (49) | 21 (19) | 28 (23) | | (30,0 p.a.) |
| ADULT FEMALES | 91 (36) | 64 (35) | 69 (33) | 68 (36) | 469 (35,3) |
| TERRITORIAL MALES | 15 (6) | 14 (8) | 13 (6) | 14 (7) | 85 (6,4) |
| PERIPHERAL MALES | 12 (5) | 3 (2) | 11 (5) | 12 (6) | 50 (3,8) |
| FEMALES/MALE | 3,14 | 3,20 | 3,00 | 2,62 | 3,17 |
| JUVENILES/FEMALE | 0,97 | 1,13 | 1,28 | 0,60 | |
| ANNUAL RAIN | 199 | 301 | 410 | 186 | |
| SEPT - NOV RAIN | 61 | 55 | 211 | 11 | |

The proportion of juveniles in the population (recruitment) was higher in the years with more rainfall. Rainfall during the entire gestation period (April - November) showed the closest correlation with recruitment ($r_p$=0,995), but rain falling during September to November was also closely correlated ($r_p$=0,979) and this relationship was significant to the more appropriate Spearman's rank correlation test ($r_s$=1,00; $p<0,05$). Good rains falling around the birth-pulse during the one month of November also appeared to be crucial for good recruitment ($r_p$=0,917). Exceptional rains fell in November 1989 (page 21), and this was when hyrax recruitment was maximal during the study. This was then followed by the lowest value of recruitment in the following year when early summer rains were negligible (see rainfall pattern in Figure 25).

University of Pretoria etd – Davies, R A G (1994)



Juvenile mortality at seven colonies was 32% during the first six months of 1988. Evidently mortality of both age groupings was very high during 1988 but declined thereafter. Two harem groups merged and there was a significant decline in group size over this period (t-test for matched pairs; t=2,5; p<0,05), indicating an overall population decline of 27%. Subsequently there was a slight increase during 1989 and a high production of juveniles at the end of this year. Low mortality of these juveniles led to high numbers of immatures at the end of 1990. A significant population increase might have occurred at this time had there not been such poor recruitment.

Assuming that adults in a tight group consisted of a single territorial male and the rest females, and that solitary adjacent adults were peripheral males, it is indicated (Table 5) that there was a marked reduction of peripheral males during 1988 (when high mortality occurred), followed by a return to former numbers. Numbers of territorial males (one per harem) remained fairly stable, and sex ratio approximated three adult females per adult male during the study period.

Details of the hyrax shot during October 1989 and 1990 (n=52) are given in Table 6. Age-determination of these hyrax allowed a direct and more detailed appraisal of the frequency distribution of older age classes. This age structure can be assumed to closely reflect the age structure during the birth-pulse, one month later. A life table was constructed from this survival schedule (assuming that the population had ceased to decline). The proportional contribution of the second age class was borrowed from the results of the counts (immatures are more likely to be shot), and the first age class was predicted from observed recruitment values. This age distribution is shown in Figure 24. The distribution indicates that old hyrax (8 years on) comprise 5,3% of the population. Smoothing of the frequencies indicates that old animals comprise 5,9% of the population.

TABLE 6
DATA DERIVED FROM DESTRUCTIVE SAMPLING
(percentages are given in brackets)

| | OCTOBER '89 | OCTOBER '90 | TOTAL SAMPLE |
|---|---|---|---|
| SAMPLE SIZE | 26 | 26 | 52 |
| JUVENILES (11mth) | 11 | 6 | 17 |
| SUB-ADULTS (23mth) | 6 | 8 | 14 |
| ADULTS (35-95mth) | 9 | 10 | 19 |
| OLD ANIMALS (107mth+) | 0 | 2 | 2 |
| FEMALES (excluding juvs.) | 10 | 9 | 19 |
| MALES (excluding juvs.) | 5 | 11 | 16 |
| FEMALES / MALE | 2,00 | 0,82 | 1,19 |
| No. FEMALES PREGNANT | 8 (80%) | 7 (78%) | 15 (78,9%) |
| MEAN LITTER SIZE | 2,25 (sd=0,46) | 2,86 (sd=0,90) | 2,53 (sd=0,74) |
| JUVENILE MASS (g) | 1569 (sd=204) | 1308 (sd=156) | 1477 (sd=224) |
| SUB-ADULT MASS (g) | 2565 (sd=406) | 2263 (sd=262) | 2392 (sd=353) |
| ADULT MASS (g) | 2998 (sd=361) | 2921 (sd=558) | 2954 (sd=474) |
| ADULT FEMALE MASS (g) | 3114 (sd=299) | 3390 (sd=510) | 3240 (sd=412) |
| ADULT MALE MASS (g) | 2767 (sd=419) | 2586 (sd=287) | 2640 (sd=319) |

University of Pretoria etd – Davies, R A G (1994)



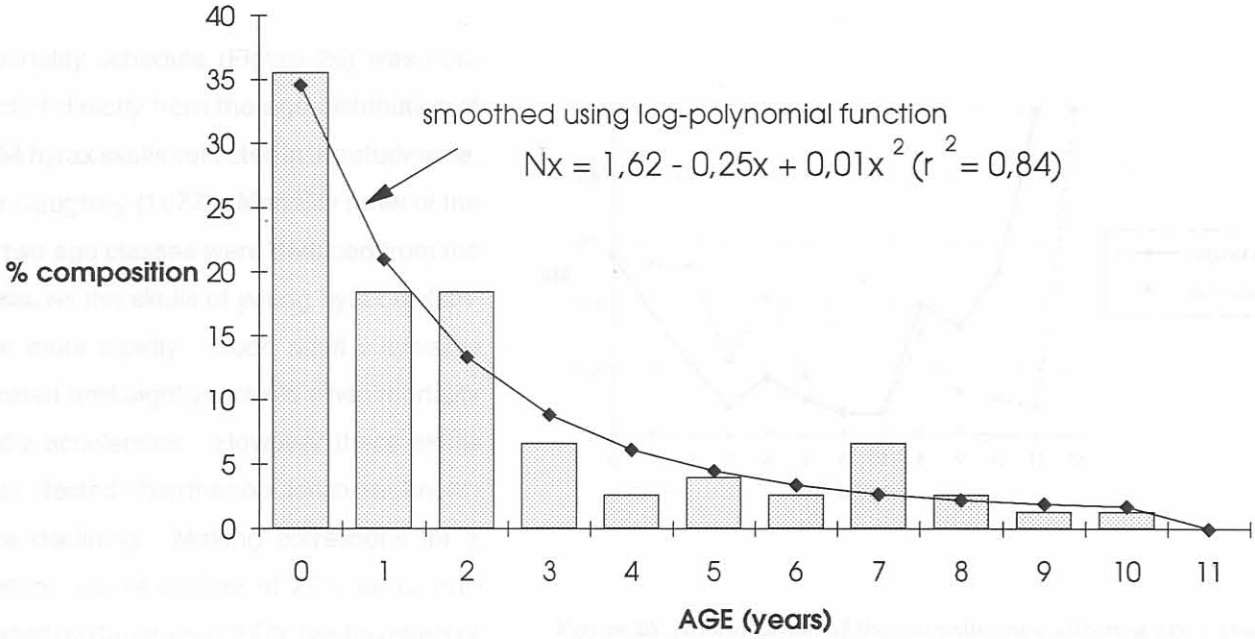



**Figure 24.** An indication of the age distribution of the rock hyrax population in the Karoo National Park 1989 - 1990, derived from age determination of 52 hyrax shot. Age classes 0 and 1 (which are likely to be biased in a shot sample) were predicted from the proportion of juveniles and immatures in the annual counts. The continuous line represents a smoothing of this distribution using the log-polynomial function as shown. However, evidence suggests this smoothing may be inappropriate (see discussion).

However, evidence suggests that this smoothing is inappropriate, and that irregularities in the distribution are real and reflect changes in the environment. The frequency distribution of estimated birth dates of the shot sample is plotted in Figure 25a with rainfall (Fig. 25b). The absence of hyrax born in 1984 from the shot sample coincides with a severe drought year. It appears rainfall affects sex ratio as well as recruitment. There was a strong correlation between the proportion of males in each birth year and rainfall during the preceding 12 months (r=-0,92; p<0.01) when the two oldest age classes were excluded. Females are known to live longer than males (Fourie 1983).

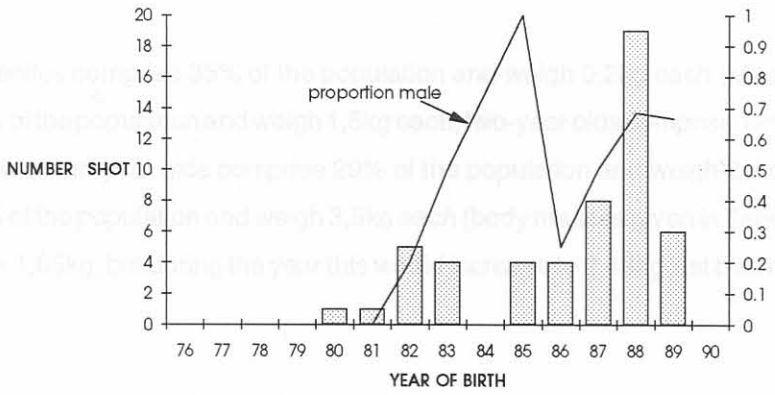



**Figure 25a.** Frequency distribution of birth dates estimated (see methods) for a sample of 52 hyrax shot 1989 - 1990; and the percentage of each cohort comprised by males (right-hand axis)

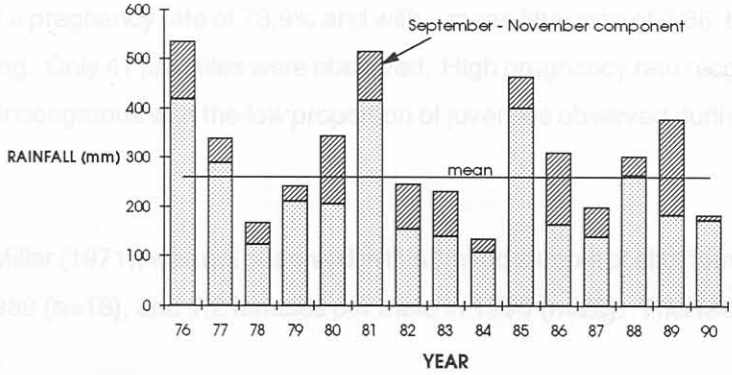



**Figure 25b.** Total annual rainfall (January to December) for the KRNP (rainfall immediately prior to the birth-pulses is shaded)

University of Pretoria etd – Davies, R A G (1994)



A mortality schedule (Figure 26) was constructed directly from the age distribution of the 54 hyrax skulls collected in the study area, after Caughley (1977). Mortality rates of the first two age classes were deduced from the counts, as the skulls of young hyrax disintegrate more rapidly. Good adult survival is indicated until eight years old when mortality rapidly accelerates. However these skulls were collected when the population was known to be declining. Making corrections for a constant rate of decline of 27% as recommended by Caughley (1977), has the effect of shifting the mortality pattern to the right (Figure 26). These mortality schedules suggest that old animals comprise 10,0% of the population, or 7,1% when corrected.

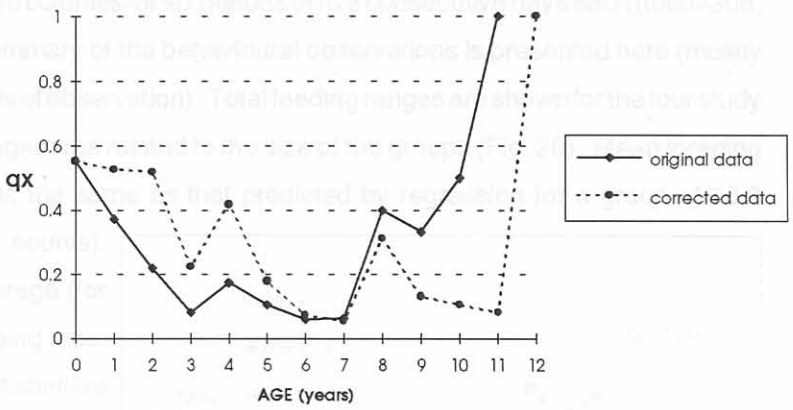



**Figure 26.** An indication of the mortality rate affecting age classes of rock hyrax in the KRNP, derived from age-determination of 54 hyrax skulls collected away from known predator feeding sites. Most of these skulls were collected during 1987. A corrected mortality rate is also shown for a population declining at a constant rate of 27% p.a., after Caughley (1977).

It is concluded that just after the birth-pulse juveniles comprise 35% of the population and weigh 0,2kg each (Millar 1971; Fairall 1980); one-year olds comprise 18% of the population and weigh 1,5kg each; two-year olds comprise 12% of the population and weigh 2,4kg each; three to seven-year olds comprise 29% of the population and weigh 2,8kg each; and eight to twelve-year olds comprise 6% of the population and weigh 3,5kg each (body masses given in Table 6). A mean mass for hyrax at this stage would be 1,65kg, but during the year this would increase to 2,43kg just before the birth-pulse.

Sex ratio of adults (>22 months) in the shot sample was one male to 1,2 females (Table 6). Assuming that this direct indication of sex ratio approaches that of the population, then 92 adults counted at the end of 1989 should be comprised of at least 50 females. At a pregnancy rate of 78,9% and with a mean litter size of 2,25 (Table 6), these females should have produced approximately 89 young. Eighty eight juveniles were observed. In 1990, 94 adults counted should be comprised of 51 females. At a pregnancy rate of 78,9% and with a mean litter size of 2,86, these females should have produced at least 115 young. Only 41 juveniles were observed. High pregnancy rate recorded in the shot sample collected in October 1990 is incongruous with the low proportion of juveniles observed during the counts in December 1990.

Precocious puberty of females as observed by Millar (1971), was not observed in this limited sample of shot females. Foetal sex ratio was 1,6 females per male in 1989 (n=18), and 1,2 females per male in 1990 (n=20). This ratio did not differ significantly from parity in either year.

University of Pretoria etd – Davies, R A G (1994)



*Behavioural observations and vegetation zones*

Four hyrax groups were observed at their respective colonies for six periods of five consecutive days each (total=30d; see Fig. 12, page 22 for details). A preliminary summary of the behavioural observations is presented here (mostly obtained from detailed analyses of just three periods of observation). Total feeding ranges are shown for the four study groups in Figure 27. The size of these feeding ranges was related to the size of the groups (Fig. 28). Mean foraging range for the four groups was 4,68ha, and this is the same as that predicted by regression for a group of 16,2 individuals (mean group size indicated by the counts). Within these ranges, groups travelled a daily average (for three observation periods) of 169 - 572m on foraging trips. Certain groups had two to three favourite over-night shelters which they used within their range. When conditions became very hot, one group moved to another refuge site on a cooler slope. Two of the groups showed overlap in their ranges with those of non-breeding groups (one or two individuals). There was no indication of overlap between the ranges of harem groups (but adjacent harems were not intensively studied). Hyrax foraging behaviour could be

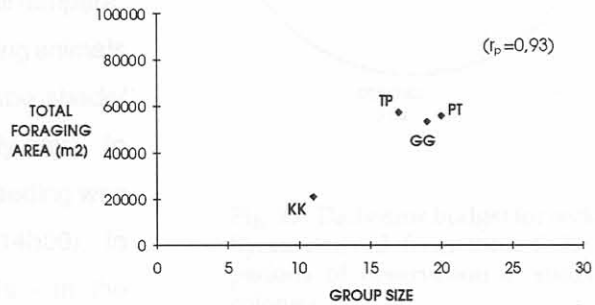



**Fig. 28.** The relationship between group size and foraging range for four hyrax study groups.

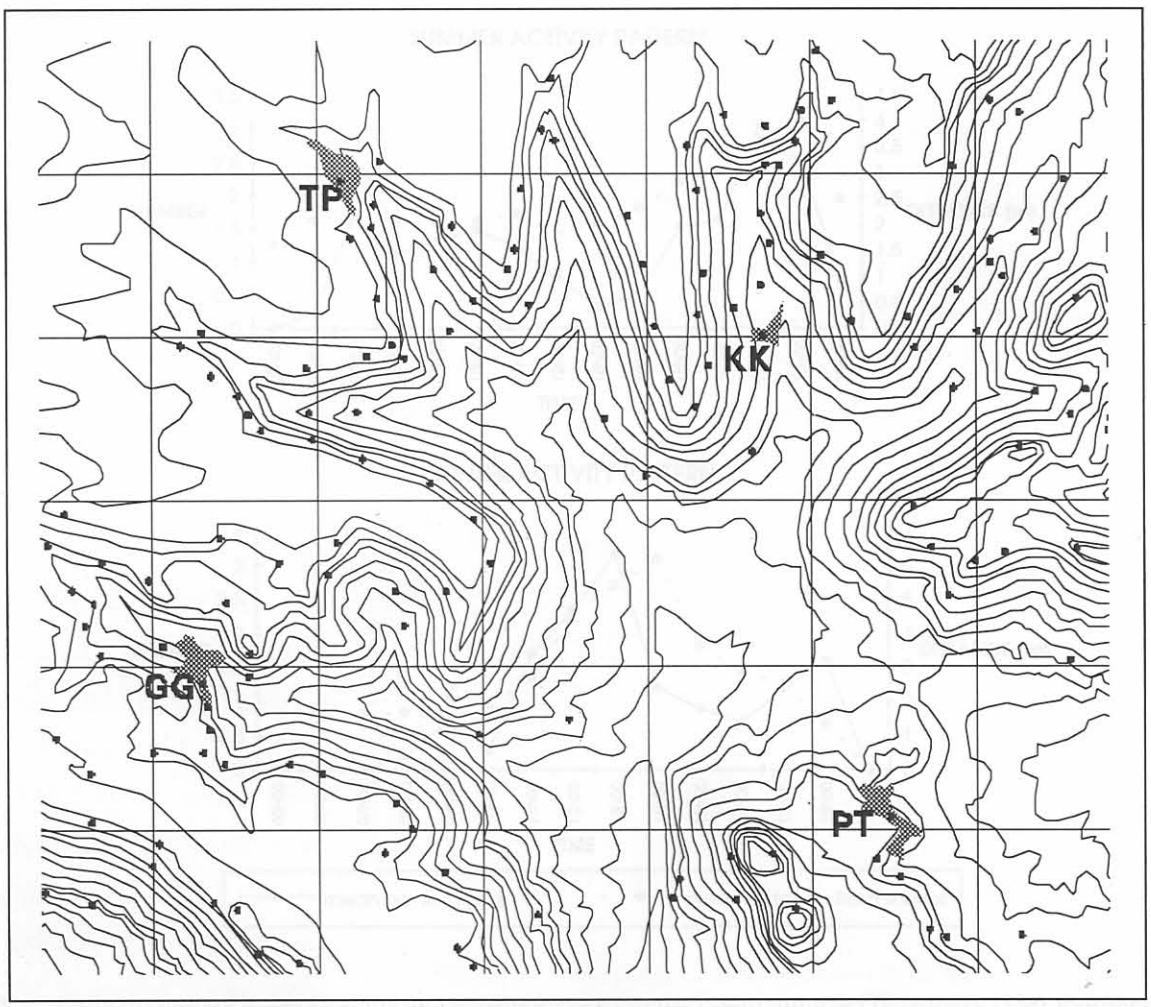



**Figure 27.** Total foraging ranges of the four chosen hyrax study groups, shown in relation to other groups (and 100' contours) in the Stolshoek region of the KRNP.

University of Pretoria etd – Davies, R A G (1994)



separated into casual feeding by individuals in the immediate vicinity of the colonies, and concerted group-feeding when all members of the group travelled some distance from the colony and fed intensively for an hour or two, usually in riparian thicket (after Sale 1965, Fourie 1983). Average daily time spent feeding by hyrax, for three of the five-day periods, ranged from 1,2h to 2,2h (see Fig. 29 for time budget), but casual feeding was not synchronised and individuals could be seen feeding over 3,5 - 7,5h of the day. Most of the time hyrax were resting in close proximity to their shelters. Sitting and huddling in the sun were the preferred postures until temperatures rose above 17°C usually at about 09h00. Thereafter, resting animals were usually lying down, sometimes half in the sun, or in the shade/ shelters on hot days. Hyrax preferred to sit or stand on windy days. In winter, hyrax spent most of the morning sunning, and group-feeding was usually concentrated in one early afternoon bout (peak at @14h00). In summer, hyrax usually conducted two group-feeding bouts - in the mornings (08h30 peak) and late afternoon (17h30 peak), to avoid the hot midday period (Fig. 30). But this behaviour pattern was influenced by changeable weather conditions and by the proximity of riparian thicket.

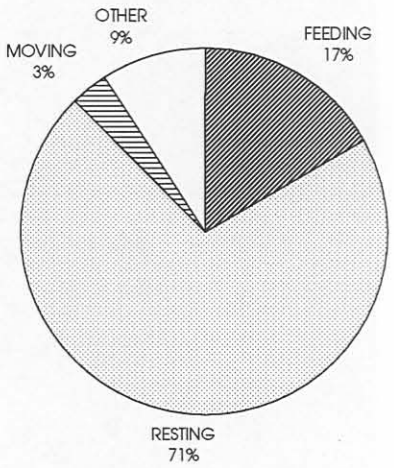



**Fig. 29.** Daily time budget for rock hyrax derived from three 5-day periods of observation at study colonies.

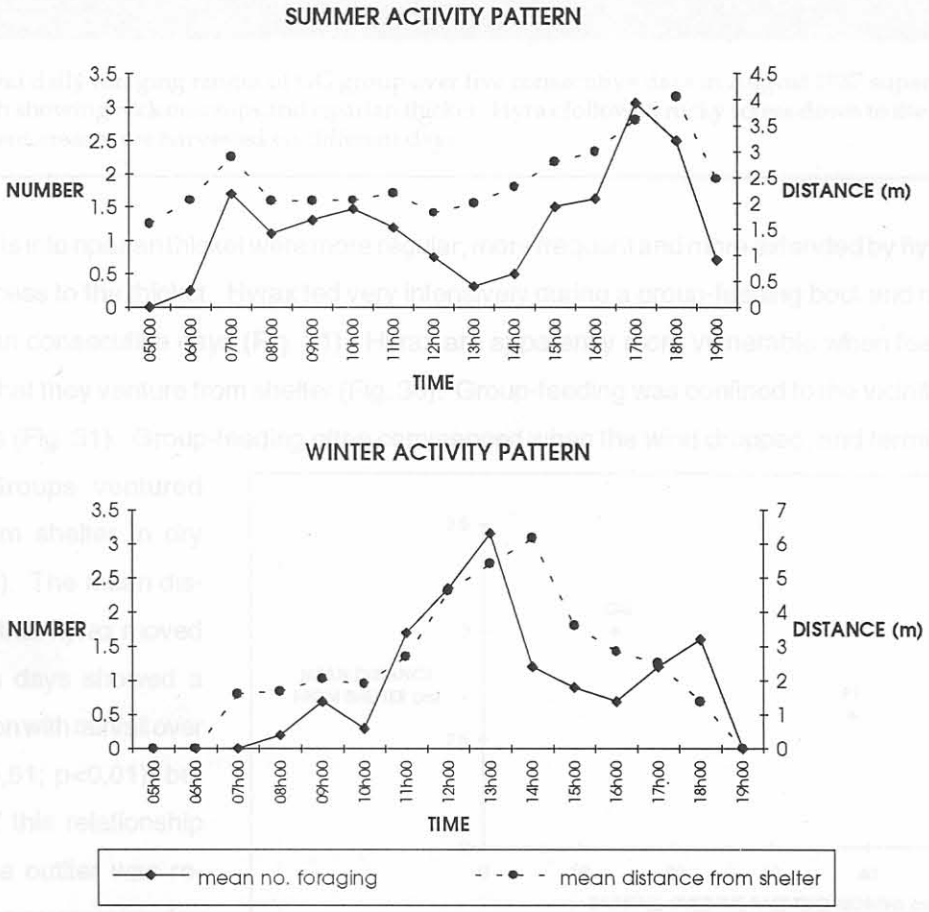



**Figure 30.** Daily rhythms of hyrax foraging movements for two groups: one in summer (TP January 1988); the other in winter (GG August 1987). The average pattern over five days is shown in each case, so peaks tend to be dampened by irregularities.

University of Pretoria etd – Davies, R A G (1994)



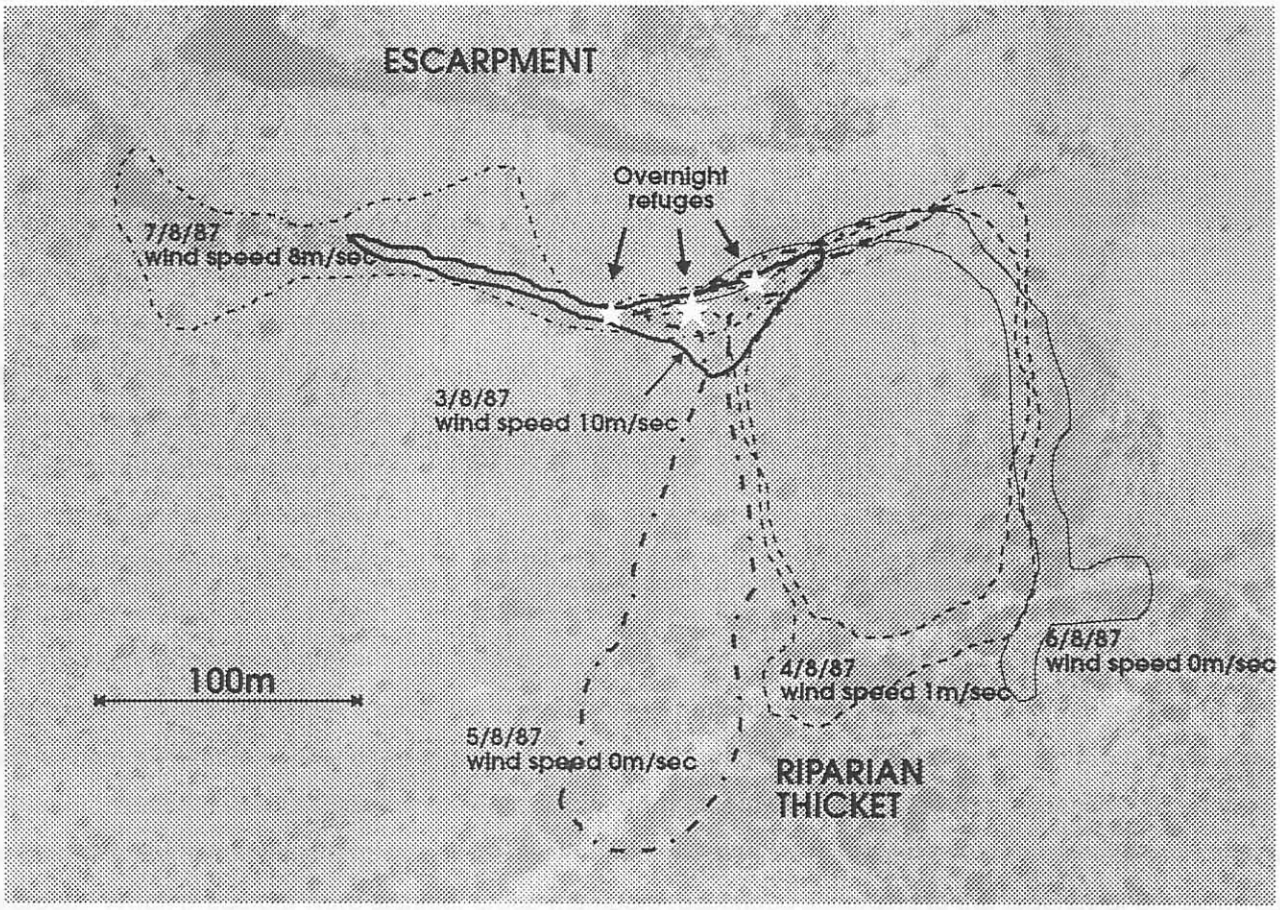



**Figure 31.** Total daily foraging ranges of GG group over five consecutive days in August 1987 superimposed on an aerial photograph showing rock outcrops and riparian thicket. Hyrax followed rocky screes down to the river course on still days. Different areas were harvested on different days.

Group-feeding bouts into riparian thicket were more regular, more frequent and more extended by hyrax groups which had close, safe access to the thicket. Hyrax fed very intensively during a group-feeding bout and nearly always fed in different areas on consecutive days (Fig. 31). Hyrax are apparently more vulnerable when feeding because of greater distances that they venture from shelter (Fig. 30). Group-feeding was confined to the vicinity of colony rocks on very windy days (Fig. 31). Group-feeding often commenced when the wind dropped, and terminated when high winds began. Groups ventured slightly further from shelter in dry conditions (Fig. 32). The mean distance from shelter that hyrax moved on 27 observation days showed a significant correlation with rainfall over the past 40d ($r=-0,51$; $p<0,01$), but the significance of this relationship was lost when one outlier was removed representing a very rainy day when hyrax remained in their shelters ($r=-0,37$; $p<0,07$).

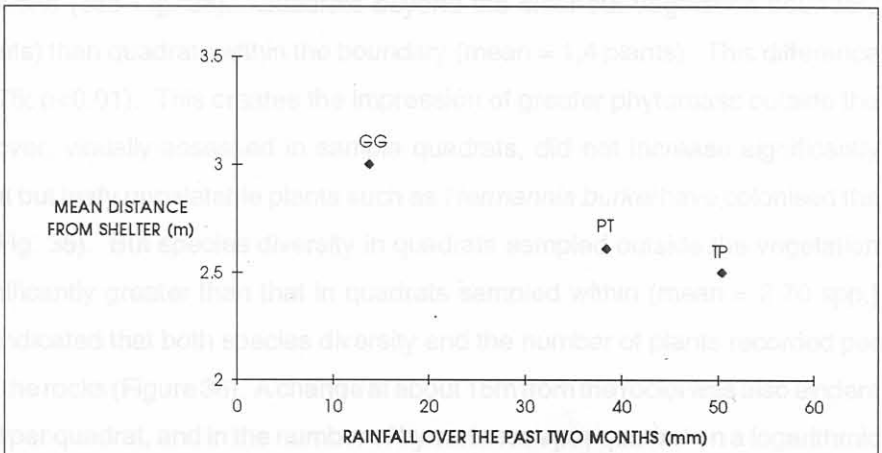



**Figure 32.** Average distance ventured from shelter for three groups over five days each, in relation to rainfall experienced over the past 8w.

University of Pretoria etd – Davies, R A G (1994)



For three periods of observations analysed thus far (2256 individual sightings), hyrax spent 96% of their time within 5m of shelter and were not observed to venture further than 15m from sanctuary (Fig. 33). Individual hyrax spent 27 - 34% of their day in a vigilant posture. Fewer animals were vigilant during group-feeding. At such times certain individuals adopted sentinel behaviour. Some recognisable individuals regularly adopted this role. They were always adults. Adult males tended to be pre-occupied with interactions with females and rival males. On one occasion a peripheral male (as defined by Fourie & Perrin 1987b) failed to warn the feeding group of an approaching Cape wildcat which it had clearly seen. It is inferred that adult females did most of the sentinel behaviour. Sentinels were in place for 20 - 37% of the time, especially when the group was travelling to and from feeding grounds. Sentinels appeared particularly vulnerable when running to catch up with the group. When predators were sighted, group members responded according to the urgency of the alarm call - usually either freezing and looking toward the sentinel or immediately fleeing for cover. Hyrax could easily distinguish between eagles that were hunting and those that were engaged in other activities (such as territorial interactions), and would take appropriate action. Hyrax were observed to employ group defence when a booted eagle *Hieraaetus pennatus* captured a juvenile (Davies 1989), but did not employ these tactics against black eagles. The intensive and casual feeding by hyrax in close proximity to rocks results in a distinct vegetation zone around regular colony rocks which is clearly visible from the air. Immediately after good rains a verdant green flush of vegetation can be seen at the entrances to rock crevices, but this soon disappears. At most colonies a clear vegetation change is permanently evident 11 - 17m from the rocks. The inner zone becomes particularly contrasting when grass growing beyond becomes lignified (yellow) in dry conditions (see Fig. 34). Quadrats beyond the clear-cut vegetation boundary contained more grass (mean = 11,5 plants) than quadrats within the boundary (mean = 1,4 plants). This difference was statistically highly significant ($F=6,75$; $p<0,01$). This creates the impression of greater phytomass outside the vegetation boundary. However leaf cover, visually-assessed in sample quadrats, did not increase significantly beyond 15m. This is because infrequent but leafy unpalatable plants such as *Hermannia burkei* have colonised the heavily grazed inner vegetation zone (Fig. 35). But species diversity in quadrats sampled outside the vegetation boundary (mean = 4,52 spp.) was significantly greater than that in quadrats sampled within (mean = 2,70 spp.) ($z=7,91$; $p<0,01$). Vegetation analysis indicated that both species diversity and the number of plants recorded per quadrat show change at about 15m from the rocks (Figure 36). A change at about 15m from the rocks was also evident in the proportion of plant shoots cropped per quadrat, and in the number of hyrax faeces per quadrat on a logarithmic scale (Fig. 37). These results are in agreement with direct observations of the distance that hyrax move from shelter (Fig. 33). Edible phytomass was estimated to be 30% greater beyond the 15m boundary.

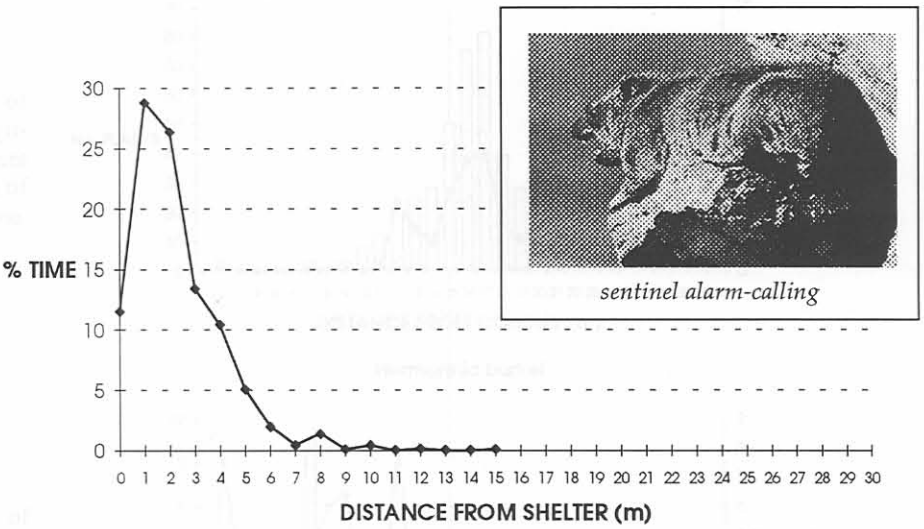



**Figure 33.** The amount of time that rock hyrax spend at varying distances from shelter. It should be noted that this analysis is based on 2256 sightings of individuals at three colonies over 15d, and only refers to hyrax which are visible outside or in the entrances to their crevices during the daytime.

University of Pretoria etd – Davies, R A G (1994)



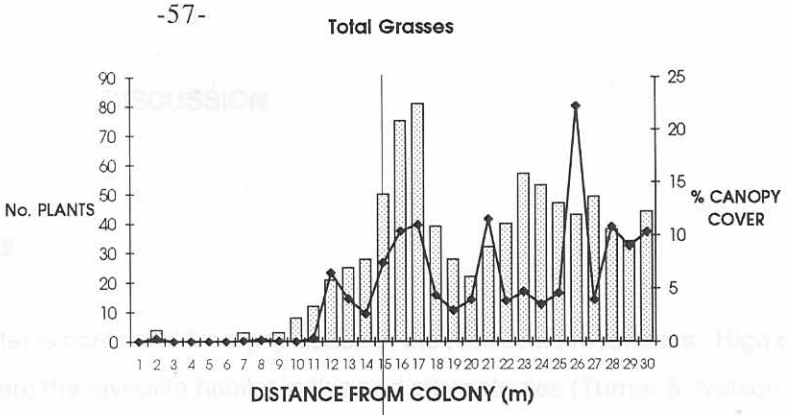



**Figure 34.** Change in the amount of grasses at increasing distance from a regular hyrax colony: number of grass plants per quadrat as columns; the proportion of quadrat area covered by grass leaf as a line.

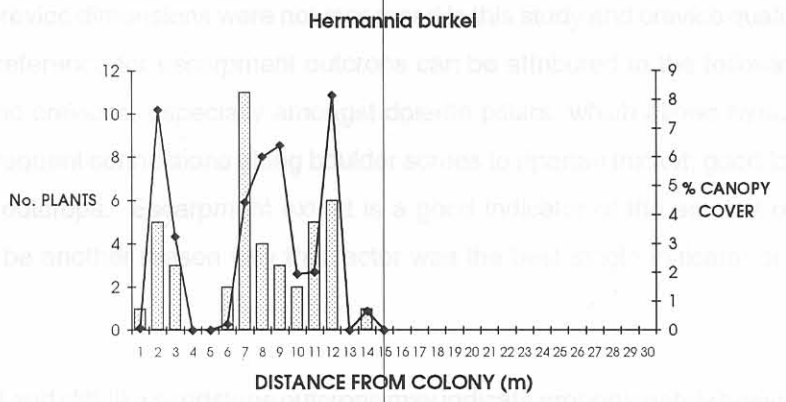



**Figure 35.** Change in the amount of *Hermannia burkei* at increasing distance from a regular hyrax colony: number of plants per quadrat as columns; the proportion of quadrat area covered by leaf as a line.

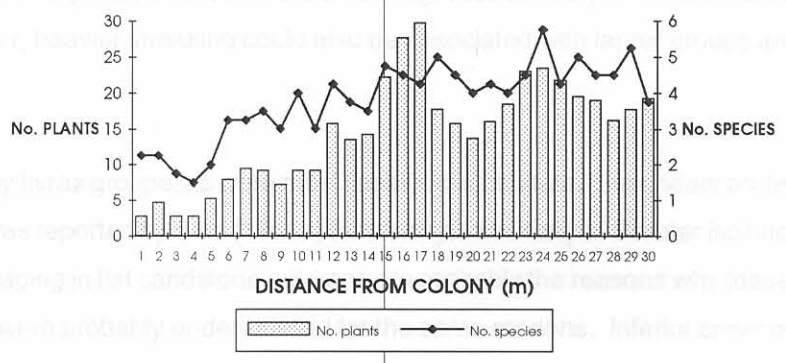



**Figure 36.** Change in the number of plants and the number of species per quadrat at increasing distance from a regular hyrax colony.

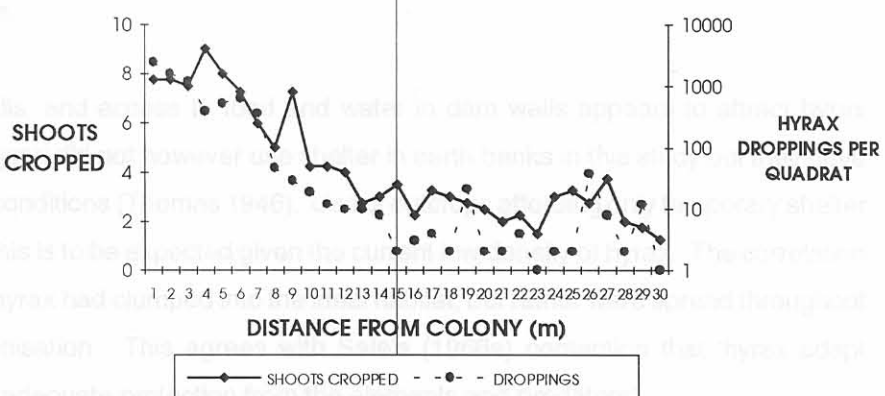



**Figure 37.** Change in the number of hyrax faeces (logarithmic scale), and in the index of cropped shoots (see methods) per quadrat at increasing distance from a regular hyrax colony.

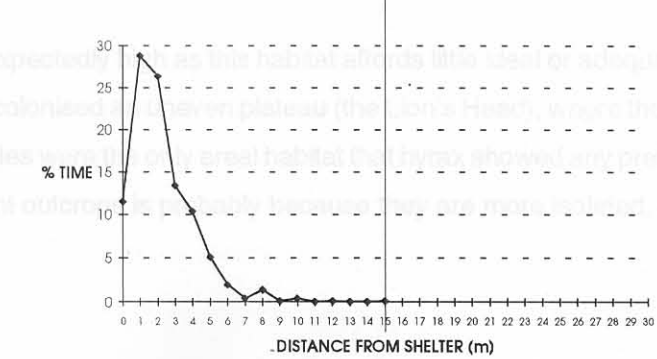



**Figure 33 duplicate.** The amount of time that rock hyrax spend at varying distances from shelter. (see previous page for full legend)

University of Pretoria etd – Davies, R A G (1994)



# DISCUSSION

*Distribution and the use of refuge habitats*

The reliance of *P. capensis* on rocky shelter is confirmed for a population in the Nuweveld mountains. High quality crevices in hard igneous rock outcrops were the favourite habitat in this and other studies (Turner & Watson 1965; Sale 1966a; George & Crowther 1981). Crevice dimensions were not measured in this study and crevice quality can only be speculated on. The observed preference for escarpment outcrops can be attributed to the following: an extensive distribution of deep fissures and crevices, especially amongst dolerite pillars, which allows hyrax safe access to a wide and rich foraging area; frequent connections along boulder screes to riparian thicket; good lookout points; and close association with other outcrops. Escarpment extent is a good indicator of the amount of rock outcrops on a given slope, and this may be another reason why this factor was the best single indicator of hyrax density.

Heavy whitewash streaking of escarpment and cliff-like sandstone outcrops may indicate proportionately heavier use of these habitats in the past. Disease or over-exploitation of food resources might conceivably have caused a recent shift into less traditional habitats. However, heavier streaking could also be associated with larger groups and well used lookout posts on tall cliffs.

Sandstone outcrops were also favoured by hyrax groups, as were most lineal rocky habitats. Secondary preference for metamorphic and sedimentary rocks was reported by Sale (1966a) for rock hyrax in Kenya. Greater isolation and fewer (smaller?) crevices to allow safe foraging in flat sandstone outcrops are probably the reasons why these were less used than cliff-like outcrops. Dykes were probably under-utilised for the same reasons. Inferior crevices may be characteristic of vertical dolerite flows.

Abundance of shelter in man-made walls, and access to food and water in dam walls appears to attract hyrax colonisation of these limited habitats. Hyrax did not however use shelter in earth banks in this study but they have been known to do so under high density conditions (Thomas 1946). Use of outcrops affording only temporary shelter as colonies was very rarely observed. This is to be expected given the current low density of hyrax. The correlation analyses however, did not indicate that hyrax had clumped into the ideal habitat, but rather were spread throughout any habitat deemed adequate for colonisation. This agrees with Sale's (1966a) contention that 'hyrax adapt themselves to any shelter that provides adequate protection from the elements and predators'.

Use of dolerite surface outcrops was unexpectedly high as this habitat affords little ideal or adequate shelter. Most groups observed in this habitat type had colonised an uneven plateau (the Lion's Head), where the atypical surface outcrops resembled small koppies. Koppies were the only areal habitat that hyrax showed any preference for. That they were less preferred than escarpment outcrops is probably because they are more isolated, and provide less access to food.

University of Pretoria etd – Davies, R A G (1994)



Avoidance of rocky screes was expected, but this habitat still offers safe foraging routes to hyrax. Low use of boulder screes (rich in food and shelter) was not expected. Other researchers (Sale 1966a; Fourie 1983) suggested that this habitat was highly favoured, but did not provide quantitative evidence. This impression may be partly due to hyrax using boulder screes for foraging during the day but retreating to colonies in lineal outcrops at night (pers. obs.; Fairall pers. comm.). Time spent in the different habitats might offer a more complete impression of habitat use than that presented in this article.

Furthermore, density of screes did not prove to be a useful variable in attempts (regression models) to explain hyrax density. While screes offer safe foraging access to hyrax, evidently they are seldom used for colonies. Crevice quality is probably the reason for this. Gaps between boulders and the substrate are unlikely to afford as much space or shelter from the elements as deep fissures in the escarpment.

Comparing the surface area of a continuous stretch of lineal outcrop with the surface area of a discontinuous areal outcrop is not strictly fair, as the latter is not a true reflection of rock surface area. Some of the preference of continuous over discontinuous habitats must be attributed to this bias, but compensation is unlikely to have changed the order of habitat choice.

Differences in the use of the major topographical habitats by hyrax are largely consequential to the outcrop preferences described thus far. Slopes were favoured because they offer most of the rocky habitat (especially lineal outcrops and screes). They afford safer access to favourite foraging areas (e.g. *Acacia karoo* in riparian thickets) along an inter-connected network of lineal outcrops and screes (outcrops on plains and plateaus are usually scattered or isolated). Slopes also offer more tall shrubs as browse - especially the highly preferred (Sale 1965; Fourie 1983) *Grewia* spp. which are common around chosen outcrops (pers. obs.). Low use of the more rocky middle plateau might be due to patchy distribution of refuge, scarcity of riparian thicket, a high grass cover, and lookouts might be less effective on flat ground.

Richer vegetation on the upper slopes did not appear to induce preference of this habitat over lower slopes. The reverse situation can be explained by the high densities of hyrax groups in kloofs which make up a significant component of the lower slopes. Easy access between converging escarpment (good overnighting) and dense boulder screes and riparian thicket (good foraging) in kloofs allows close siting of large hyrax groups. Kloofs often also provide a source of water.

There was no evidence in this study that hyrax avoided the hot (and grassy) north-facing slopes unlike red rock rabbits (see next chapter). The distribution of Alpine marmots was found to be influenced by related thermoregulatory constraints (Turk & Arnold 1988), but hyrax groups in the KRNP have the ability to move when conditions get too hot. One would expect east-facing slopes to be favoured by hyrax because the early sun on these slopes affords an extra couple of hours foraging, therefore it seems reasonable to accept the one-tail statistical test which demonstrated the preference of hyrax for east-facing over west-facing slopes. There was no clear evidence in this study that strong wind prevented colonisation of certain slope aspects as observed by Sale (1966a), but wind did inhibit foraging behaviour.

University of Pretoria etd – Davies, R A G (1994)


*Demography*

The majority of rock hyrax in the Nuweveld mountains exist in many similar-sized groups spread out through the available habitat. The size of these groups must be subject to various constraints: as groups become larger, competition for food and shelter increases (Hoeck *et al.* 1982); and increased aggression in less-cohesive large groups might cause social disruption with male monopolies unsuccessful and some females unmated (e.g. Downhower & Armitage 1971). A decrease in group size however, may lead to inbreeding and greater predation risk (especially of young) through lowered vigilance, guarding and defence (e.g. Rasa 1986). One would expect that a trade-off of these various constraints would result in an ideal group size.

The relationship between group size and habitat observed in the study population probably results from competition for food and shelter in the presence of predation. Groups were larger in habitats such as escarpment pillars and boulder screes, where an abundance of large crevices allows safe access to a wide foraging range (non-breeding animals may be coerced out of these favourite habitats). Sparse crevices along flat sandstone outcrops and dykes probably cannot accommodate large groups. Large groups in boulder screes coped with inferior crevices by fragmenting, perhaps encouraging the formation of complexes in this habitat. Most multiple-harem groups occurred in kloofs where a source of abundant food and perhaps water reduces the constraints operating on increased group size, and where a dense and complicated distribution of crevices can accommodate high numbers and splinter groups. Male monopolies would be more difficult to maintain under these conditions.

Despite these influences, there was a distinct central tendency in the study population for harem groups to approach 16,4 individuals. This group size is probably advantageous in this environment. It is smaller than that observed by Fourie (1983) in the Mountain Zebra National Park (MZNP), and by Hoeck (1982) in the Serengeti, both higher rainfall areas where more rapid renewal of resources would permit larger groups. Use of this mean group size to determine a population estimate is preferred to the habitat sampling method for the following reasons: group-plotting was a more direct and extensive indication of the population; the distribution of hyrax was not very predictable for extrapolation; and habitat strips had to be chosen for practical reasons rather than randomly. Simple extrapolation of hyrax density with the extent of rock outcrops would over-estimate hyrax numbers in situations where two refuge habitats occur in close proximity to one another and where certain hyrax groups are mobile between both habitats.

In 1984 hyrax density in the KRNP was estimated at 72 - 94km$^{-2}$ (Fairall *in litt.*). This was probably during the widespread decline (Chapter 1), for numbers apparently declined further by the time of this study. The deduced density (35,2km$^{-2}$) for the study area in 1989 was far lower than that (376km$^{-2}$) crudely estimated for the MZNP by Fourie (1983). The latter study was carried out in a wetter area prior to the widespread decline. Hyrax biomass in the most favoured kloofs (3,7kgha$^{-1}$) was lower than the recommended carrying capacity for sheep in the area (@16kgha-1), and did not even approach the extraordinary biomass levels (26-109kgha-1) recorded for two rock hyrax species inhabiting Serengeti koppies (Hoeck 1982). However, these latter estimates are misleading as the full foraging ranges of the animals (which included some of the surrounding grassland) were not taken into account.

University of Pretoria etd – Davies, R A G (1994)



The sample of shot hyrax gave the only direct indication of population composition. The shot sample indicated a much more even adult sex ratio (1,2 females per male) than that indicated by interpretation of the group counts (3 females per male) or that recorded by Fourie & Perrin (1987b) from livetrapping at colonies in the MZNP (2,4 females per male, during November). Bias in sampling adult males or females is unlikely. The high incidence of males in the shot sample suggests that the groups must have contained more than one adult male each. It is possible that adult males were being retained in groups in a sexually quiescent state (as observed by Hoeck *et al.* 1982; van der Merwe & Skinner 1982) in order to maintain an advantageous group size under low density conditions. Small groups would suffer especially high predation at low density. Peripheral males largely disappeared during 1988, they may have been incorporated into the groups. It is relevant to note that of the two colonies monitored by Fairall (*in litt.*) which both supported more than 20 hyrax initially (1981), the more exposed site (Die Gat) experienced a more drastic decline (to zero) and did not recover beyond a few individuals, while the more established and protected colony (Moordenaarsgat) did not drop below 9 individuals and had returned to former numbers by 1987.

High mortality of juveniles (@55%p.a.) recorded in this study appears to be commonplace (Fourie 1983). Juveniles suffer high predation pressure from a very wide variety of predators (e.g. Davies 1989), and this may have contributed to the evolution of a restricted breeding season (unexpected in unpredictable environments). Juvenile mortality was lighter during 1989 following heavy summer rains. Fourie (1983) witnessed similar effects in the MZNP and used population models to demonstrate the profound influence of variable juvenile mortality on hyrax population dynamics.

The heavy mortality evident during 1988 might have been linked with the earlier widespread decline. This earlier decline coincided with extremely high losses of springbok at two localities in the Karoo (Davies 1985; Liversidge pers. comm.) and of other ungulates in southern Africa (Knight pers. comm.; Williamson & Mbano 1988), suggesting a strong link with drought. Fairall (*in litt.*) stressed the importance of drought and increased predation as causative agents for the hyrax decline. Summer rains at the beginning of 1988 and at the end of 1988 were both below average for the KRNP, so 1988 could be considered a year of drought.

Skulls collected in the KRNP were the most direct indication of mortality pattern and suggested good adult survival until eight years old - this is when dental attrition becomes apparent. The evidence suggests a stable age structure with old animals comprising a small fraction (6-7%) of the population. Numbers of old animals were exaggerated by interpretation of the skull collection, unless corrected for a declining population.

The erratic karoo rainfall appeared directly responsible for annual variation in hyrax recruitment, and thus population structure. This relationship may have been more responsible for irregularities in the age distribution than the variable mortality (which can affect all age classes). Evidence for this relationship came from the distribution of birth dates in the shot sample as well as from the annual counts. Better recruitment in wetter conditions has been recorded for hyrax in other karoo localities (Millar 1971). Rainfall preceding the birth-pulse showed a very close relationship with recruitment. Moist vegetation from recent rains is probably important for lactating females.

Mean litter size recorded in this study was quite similar to that recorded elsewhere in the Karoo (Van der Horst 1941; Millar 1971; Fourie & Perrin 1987a). Fecundity data from the shot females suggested that the number of juveniles

University of Pretoria etd – Davies, R A G (1994)



counted at the end of 1989 was a close measure of the number of juveniles actually born that year. But this is only an indication, and the adult sex ratio used in the fecundity calculation was based on a limited sample. The number of juveniles seen is likely to be a slight underestimate of recruitment. Higher fecundity of females shot one month prior to the 1990 birth-pulse was probably due to exceptionally good rains the previous summer, but it was incompatible with the low number of juveniles observed in December (which were confirmed by repeated counts). Nineteen ninety was particularly dry with very little rain falling between September and November. The low number of juveniles observed might either be due to early infant mortality within the crevices (this is unlikely to pass unseen as juvenile rock hyrax emerge on their first day, Millar 1971), or to late foetal loss - by resorption or mummification *in utero*. Higher foetal loss was observed in dry conditions by Millar (1971) and Fourie (1983), the latter reported one incidence of late foetal resorption. The ability to resorb foetuses at a late stage would be highly adaptive for hyrax in an unpredictable environment.

The relatively high incidence of adult males in the study population, as indicated by the shot sample, appears to be an effect of drought. Within the shot sample, males predominated in age classes that were born during dry conditions, while females predominated in age classes that were born during wet conditions. The study was preceded by a major drought. Greater neonatal size of males (Millar 1971) might confer greater survival of male offspring in dry conditions, but should not confer greater survival of female offspring under wet conditions. It is possible that more males were born during dry conditions, and the sex ratio amongst foetuses collected in the very wet year of 1989 (1.6 females per male, n=18) suggests that more females are born in wet conditions. More data on this topic are considered in Chapter 10. Further, large-scale collections are needed to confirm these indications but sex-biased offspring have been observed for a variety of mammals (Simpson & Simpson 1982; Verme 1983: Clutton-Brock 1985), and even for birds (Dijkstra, Daan & Buker 1990).

The relationship between rock hyrax foetal sex ratio and rainfall as suggested here may simply be an effect induced by the environment (e.g. through timing of breeding, or differential likelihood of resorption for different-sized foetuses). But the studies listed above have often linked biases in foetal sex ratio to the social status or body condition of the mother, and adaptive explanations are offered. In keeping with Clark (1978), female rock hyrax suffering from the effects of local resource depletion should produce more sons (which are likely to disperse) than daughters (which are likely to remain and antagonise local resource depletion). However, Armitage (1987) suggests that such explanations should be based on the long-term reproductive potential of the offspring.

Male hyrax have a greater reproductive potential than females if they can overcome the risks incurred by predation during dispersal, and from agonistic encounters during establishment. In populations known to fluctuate markedly, male dispersal should be most successful at the start of a population decline (during drought) when predation risk would still be low (at high density), and when prospects for establishment should begin to increase. The risk of predation for dispersing male hyrax may also be reduced during dry conditions if all hyrax are forced further from their rocks to feed.

The dramatic response of hyrax mortality and recruitment to a variable climate results in an irregular and a very dynamic population structure. Smoothing of the age distributions and the use of life tables to generalise about this structure would only be valid for a hypothetical hyrax population in a constant environment.

University of Pretoria etd – Davies, R A G (1994)



*Behaviour*

By feeding very intensively and synchronously during group-foraging bouts, and by routinely using different parts of their range on consecutive days, hyrax groups make extremely efficient use of the time that they spend away from the safety of their colony rocks. This efficiency effectively enables hyrax to minimise risky foraging behaviour (Sale 1965). Other researchers have noted that hyrax groups may travel 500m down slopes in order to forage in riparian thicket (Fourie 1983). A rich food supply and a relatively safe feeding environment in riparian thicket are the most probable explanations for this behaviour and for the tendency for colonies to be located near to river courses (Fig. 22). Sale (1965) noted that the distribution of hyrax groups in the Mackinder Valley was more influenced by vegetation quality (along streams) than by availability of refuge. Daily time allocated to feeding by hyrax in this study (2,06h) was slightly lower than that recorded elsewhere in a wetter region (2,4h - Fourie 1983), and this is suggestive that hyrax in the present study were not unduly stressed by food availability. This is to be expected given low hyrax densities and reasonable rainfall. Even so, there was some indication of groups venturing further from shelter when conditions were drier and this is supportive to Allan's (1988) speculation on variation in the availability of prey to black eagles (page 26).

Sentinel behaviour was not apparent all the time, and was only obvious during group-foraging bouts. This is when hyrax are probably most vulnerable to predation because they venture furthest from shelter and fewer individuals are vigilant. Alarm-calling is a very effective anti-predator behaviour for rock hyrax. Group members showed synchronised and well-defined responses to particular calls (as observed by Sale 1965), and it seems likely that the alarm calls convey much information on the nature of the attack as has been demonstrated for dwarf mongooses *Helogale undulata* (Beynon & Rasa 1989). It was clear though that only certain individuals proved effective at alarm-calling. Failure of low-ranking individuals to warn of danger as observed in this study has also been witnessed in vervet monkey *Cercopithecus aethiops* groups where withholding information may construe some long-term advantages to the individual (Cheney & Seyfarth 1985). An essential condition for the effectiveness of these 'early warning systems' is obviously that the alarm should be clearly audible to group members. Ineffectiveness of alarm calls is probably a major reason why hyrax did not venture far from sentinels under very windy conditions and why they did not enter riparian thicket on such days. However black eagle activity is also enhanced on windy days (Chapters 6 & 8).

High nitrate concentrations in hyrax faeces probably enable strong germination of seeds in the faeces and thus give rise to the verdant flush of vegetation around rock crevices after good rains. The same phenomenon has been observed around woodchuck *Marmota monax* burrows (Merriam & Merriam 1965). Hyrax are probably least vulnerable to predators when they can graze this luxuriant vegetation literally at their doorsteps. Predominance of unpalatable plants close to refuge sites is also a common effect of heavy grazing by small herbivores (Farrow 1917; Koford 1958; Huntly, Smith & Ivins 1986). Central-place foraging theory (Orians & Pearson 1979) predicts this, and also that plant abundance and plant species diversity should increase with distance from refuge, as observed in this study. One might expect that hyrax would feed more selectively further out from shelter in keeping with predictions and other studies (e.g. Huntly *et al.* 1986). Most studies of vegetation patterns around refuge sites used by small herbivores indicate either multiple vegetation zones radiating outward (Farrow 1917; Koford 1958; Merriam & Merriam 1965) or a gradual / clinal change in plant composition (Hall 1960; Huntly *et al.* 1986; Huntly 1987), and this is in keeping

University of Pretoria etd – Davies, R A G (1994)



with predicted gradual changes in travel costs and in accessible feeding area (Huntly 1987; Fig. 38). However in this study, various lines of evidence point to one major vegetation zone and a clear cut-off in feeding at about 15m from refuge. This cut-off boundary appears very distinct, especially with regard to the distributions of palatable and unpalatable plants. It begs the question of why the hyrax do not travel 16m from the rocks and access a much richer food supply, and it suggests that some other factor is restricting their movements. I would speculate that the cut-off in feeding at 15m represents a trade-off between increased foraging return and increased risk of predation. The apparent absence of this phenomenon in other small, refuging herbivores may be due to the fact that most of these herbivores can modify their refuge environments, and / or the hyrax may be exposed to a greater degree of predation risk. Such trade-offs have been suggested to explain complex behaviour in a wide range of animals (reviewed in Lima & Dill 1990). Both direct observations and vegetation analyses indicated that hyrax prefer to feed and live within distinct confines of a refuge environment. This may lead to increased agonistic behaviour and reduced breeding through crowding effects and thus influence demography. It seems likely though that hyrax would venture from the refuge area under very high density conditions and they have been observed to do so while dispersing.

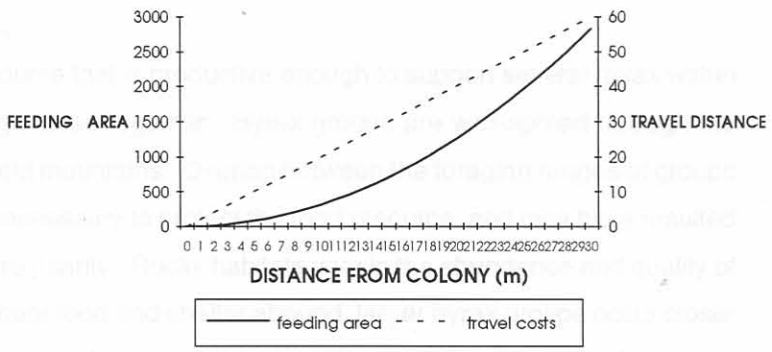



**Figure 38.** Model of how hyrax travel costs and the amount of accessible vegetation (food) would be expected to change at increasing distance from the colony rocks

*The link between caverniculous and gregarious behaviour*

Burrowing is not an option in the hard, rocky mountains of Africa where hyrax have chosen to use the abundance of rock crevices for a comfortable microclimate, shelter from predators, and safe access to a rich forage supply. To inhabit rock crevices, hyrax have become much smaller than their ancestors (Sale 1970a), and by so doing have become vulnerable to a wider variety of predators which abound in the mountainous terrain and hunt by day, including some highly mobile raptors. Furthermore, the adaptations necessary for living amongst rocks such as short legs and a stout build make hyrax relatively slow and vulnerable in the open. Hyrax can easily be outrun by humans on flat ground (pers. obs.). Hyrax cope with this vulnerability by minimising foraging time spent away from rocks, by dispersing at night, and by living in groups (enhanced vigilance and early warnings).

Groups of animals are more conspicuous but increased predator interest is countered by increased vigilance, group defence, and by making use of sentinels. Other advantages of living in groups, such as huddling and easy procurement of mates, are more likely to be spin offs of gregariousness rather than primary causes for it. The patchy distribution of suitable crevices, which are a non-depletable but limited resource may also give added incentive to share, and provides males with the opportunity to monopolise female groups by defending this discrete critical resource (see Emlen & Oring 1977). This system leads to male dispersal and female phillopatry (Clark 1978). Sociality appears to have been encouraged in marmot species living in limited environments where they take longer

University of Pretoria etd – Davies, R A G (1994)

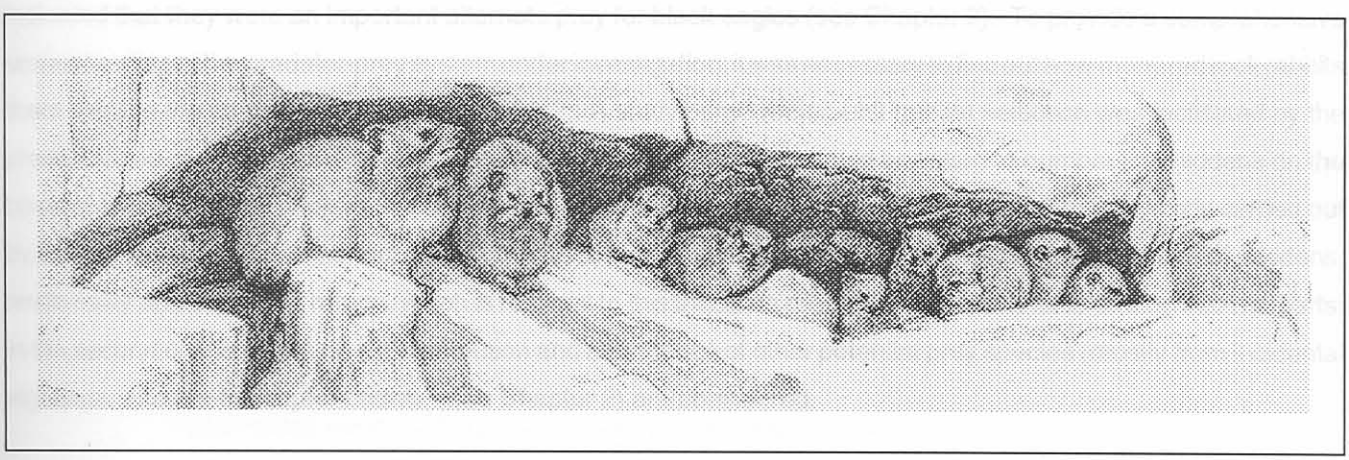


to reach a safe dispersal size, and Olympic marmots can vary the timing of their dispersal to suit environmental conditions (Barash 1974). Social tolerance amongst hyrax might be encouraged for the same reasons in the arid unpredictable climate of the Karoo. The growth rate of juvenile hyrax is markedly influenced by food supply (Millar 1971).

The variability of hyrax recruitment and mortality must drastically alter population composition in response to climatic change. The observed flexibility in hyrax social organisation to accommodate these effects demonstrates the importance of maintaining a sensible group size. This group size is probably primarily a compromise between predator detection and the availability of food and shelter.

One requirement of living in groups is for a food resource that is productive enough to support several hyrax within the individual's range and to allow animals to forage close together. Hyrax groups are well-spread through the complicated network of rocky habitats in the Nuweveld mountains. Overlap between the foraging ranges of groups appears small, territoriality between groups may be necessary to protect the food resource, and may have resulted in a group dispersion pattern which tended towards regularity. Rocky habitats vary in the abundance and quality of crevices, and in the richness of accessible food. Where food and shelter abound, larger hyrax groups occur closer together. Each group occupies part of the rocky network within which they are mobile, using outcrops with high quality crevices for colony locations, and outcrops with well dispersed crevices to access their renewable food resource.

Refuge appears to be the second major requirement for group-dwelling in hyrax-sized mammals. The increased activity of groups of animals would attract attacks from predators, especially raptors, which cannot easily be outrun. All similar-sized gregarious mammals burrow or use some form of existing shelter (e.g. King 1959; Barash 1974; Cowan & Bell 1986; Rasa 1986; Herzig-Straschil 1978). Enhanced predator detection would not be an incentive for group-dwelling if the prey could not rely on an avenue for escape. In this way, the caverniculous behaviour of rock hyrax has facilitated and maybe even encouraged gregarious behaviour and the two habits have become inextricably linked.



University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 5*

# *DISTRIBUTION AND ABUNDANCE OF ALTERNATE PREY*

## *PART 1: RED ROCK RABBITS*

### INTRODUCTION

Red rock rabbits (*Pronolagus* spp.) are nocturnal and generally solitary lagomorphs that occur in a wide range of rocky habitats in southern and eastern Africa (Ansell 1960; Smithers 1971; Peddie 1975; Skinner & Smithers 1990). They do not burrow and can often be found lying up in a form, relying on crypsis and dextrous escape over rocks to evade predators. Such habits suggest some behavioural affiliation with hares but the chromosome complement of red rock rabbits establishes their evolutionary identity as rabbits (Robinson 1981). Their small hindlimbs suggest that escape from predation involves the use of cover, rather than sheer speed (Cowan & Bell 1986), and indeed they are observed to find refuge amongst loose rocks, in rock crevices and in dense vegetation where they create an open nest and bear their altricial young (Skinner & Smithers 1990).

They are predominantly grazers (Stewart 1971) and produce copious amounts of characteristic disk-shaped faecal pellets which they deposit in regular middens (Peddie 1975; Skinner & Smithers 1990). This suggests an unselective, bulk-feeding habit which may be a consequence of restrictions on movement imposed by refuge requirements (Cowan & Bell 1986). Demographic information can often be easily obtained from regular defecation habits (Putnam 1984): faecal pellets (and pellet groups) have been successfully used to estimate abundance of deer (Davis 1982), water voles (Woodroffe & Lawton 1990), and leporids (Taylor & Williams 1956; Angerbjörn 1983; Krebs, Gilbert, Boutin & Boonstra 1987). The use of middens or latrines has been associated with territoriality in mammals as widely varying as water voles (Woodroffe & Lawton 1990), rabbits (Mykytowycz 1966), badgers (Kruuk 1978; Roper, Sheperdson & Davies 1986), deer (Green 1987), antelopes (Owen-Smith 1977) and rhinoceros (Owen-Smith 1971). Pepler (1990; pers. comm.) implicates a territorial habit in Smith's red rock rabbit, *Pronolagus rupestris*.

Smith's red rock rabbits (here-on referred to as red rock rabbits) are numerous in the KRNP, and early observations indicated that they were an important alternate prey for black eagles (see Chapter 9). To provide a comprehensive understanding of the predator-prey system under investigation, it was necessary to find out how many red rock rabbits there were in the different habitats of the KRNP. A study of red rock rabbit habitat selection was facilitated by the prevalent use of middens in this cryptic species. Numbers of rabbits could be linked to numbers of middens on the basis of faecal accumulation rates on middens. Field work and analysis for this investigation was jointly carried out by Elsabe Aucamp (for an honours project) and myself. The study also suggested a link between use of middens, territoriality and the use of refuge, which is relevant to this thesis on predation. This chapter is divided into two parts: in the second section, data on the distribution and abundance of other potential prey species (mostly from incidental sightings, and the helicopter counts - see Chapter 2) are considered.

University of Pretoria etd – Davies, R A G (1994)



## METHODS

Straight-line transects of one kilometre in length were conducted randomly in each of the major topographical habitats of the KRNP until the number of middens encountered exceeded the sample size recommended by Burnham, Anderson & Laake (1980). Approximately 18 transects were completed for each habitat except the bottom plains where no middens were encountered. The route of each transect was noted and marked out for possible future repetition. The size, perpendicular distance from the transect line and the position along the transect for each midden encountered was recorded, along with a visual assessment of the local microhabitat for each midden. The microhabitat variables recorded are described in Table 7. To compare microhabitats of the middens with microhabitats available, the same variables were recorded regularly every 250 paces along each transect line. These latter recordings also provided data for comparisons of the major topographical habitats.

TABLE 7

A DESCRIPTION OF THE MICROHABITAT VARIABLES THAT WERE VISUALLY ASSESSED FOR EACH MIDDEN AND AT REGULAR INTERVALS ALONG EACH TRANSECT LINE

| VARIABLE | RATING | DESCRIPTION |
|---|---|---|
| SLOPE | 0 | flat |
| | 1 | gentle slope |
| | 2 | steep slope |
| | 3 | sheer cliff |
| ORIENTATION | - | N, NNW, NW, WNW, W ... etc. |
| ALTITUDE | 1 | bottom plains (910m) |
| | 2 | lower slopes, gentle (988m) |
| | 3 | lower slopes, intermediate (1065m) |
| | 4 | lower slopes, steep (1143m) |
| | 5 | middle plateau (1220m) |
| | 6 | upper slopes, gentle (1373m) |
| | 7 | upper slopes, intermediate (1525m) |
| | 8 | upper slopes, steep (1678m) |
| | 9 | upper plateau (1830m) |
| LOCAL ROCK TYPE | 0 | no rocks |
| | 1 | small loose rocks (most <10cm high) |
| | 2 | large loose rocks (most >15cm high) |
| | 3 | boulder scree (most >1m high) |
| | 4 | sandstone lens outcrop |
| | 5 | surface knoll of dolerite on plateau |
| | 6 | dolerite/sandstone escarpment |
| DISTANCE TO ROCKS | m | estimated distance to nearest substantial rock outcrop that could potentially afford secure shelter to a rabbit |
| DISTANCE TO WATER | m | estimated distance to the nearest episodic water course |
| PLANT COVER | 0-9 | 0% plant cover - 90% plant cover (occular estimate) |
| BUSH:GRASS RATIO | 0-9 | 0%shrub/100%grass - 90%shrub/10%grass (occular estimate) |
| DENSITY OF LARGE SHRUBS | 0 | no large shrubs |
| | 1 | scattered large shrubs |
| | 2 | thicket |
| | 3 | dense trees |

University of Pretoria etd – Davies, R A G (1994)



Overall midden density in mountainous terrain was assessed using a fixed width transect based on the frequency distribution of middens at varying distances from the transect line. Midden densities in each of the major topographical habitats were assessed using both the model of Eberhardt (1968) for transects of indefinite width, and the Fourier series estimator for ungrouped data recommended by Burnham *et al.* (1980).

As part of an intensive, localised study, all middens (n=56) in a 12,3ha study area at Mountain View on the upper plateau were plotted on an aerial photograph. The spacing pattern of these middens was investigated using the G-statistic as described in the previous chapter (pages 39-40).

Twenty to 45 of these middens (mean=35) within the Mountain View study area were cleared of fresh faecal pellets every second day for an eight-day period in January 1990 and two further eight-day periods in July 1990. The area was also regularly screened to check for faecal pellets distributed away from middens. The literature was consulted for estimates of defecation rates of *Pronolagus* and similar species, so that faecal accumulation rate per midden could be used to indicate the ratio of animals to middens.

Further to this, three rabbits were captured on the Mountain View study area by the method of Pepler (1989), and force-fed a liquid paste consisting of a fluorescent pigment and Pro-nutro cereal (Nutri product, Milchik, R.S.A.) diluted with water. The paste was introduced past the back molars of the animal using a syringe. This stimulated swallowing and proved more successful and less risky than stomach intubation when practised on domestic rabbits. Different pigments were used for the different individuals. The rabbits were captured and released during periods of faecal pellet collections, and the collections from each midden were inspected under ultra-violet light to trace the subsequent movements and defecation rate of each treated rabbit.

A third indication of the ratio of animals to middens was obtained from energetic considerations. Mean mass for a faecal pellet was assessed in summer and winter by collecting ten pellets from each of ten middens in the Mountain View study area, and drying these at 65$^{o}$C for four days before weighing. The energy content of ten summer pellets and ten winter pellets was assessed by bomb calorimetry. From the average faecal accumulation rate, it was possible to predict the average amount of faecal energy accumulating per midden per night. The amount of energy digested that this represents was then estimated from appropriate figures of digestive efficiency obtained from the literature, and this figure was compared with predicted energy requirements of an average rabbit.

Fresh faecal pellets were collected from a further 63 middens outside the Mountain View study area during the course of line-transect sampling in order to check for differences in midden use between the major habitats. This was necessary to ascertain whether the ratio of animals to middens determined in the Mountain View study area could be extrapolated to other areas of the park.

University of Pretoria etd – Davies, R A G (1994)



# RESULTS

*Appraisal of the major topographical habitats*

Significant variation in the physiognomy of the major topographical habitats was revealed by the microhabitat assessments along the transect lines. Non-parametric, one-way analysis of variance (Kruskal-Wallis tests) showed statistically significant differences between the major habitats for the following parameters: plant cover ($X^2$=127,3; d.o.f.=4; p<0.01); bush to grass ratio ($X^2$=109,7; d.o.f.=4; p<0.01); density of large shrubs ($X^2$=97,1; d.o.f.=4; p<0.01); distance to rocks ($X^2$=83,8; d.o.f.=4; p<0,01); and distance to water ($X^2$=71,6; d.o.f.=4; p<0,01). After aggregation of appropriate local rock type categories, contingency table analysis revealed statistically significant differences between the major habitats for this parameter also ($X^2$=66,3; d.o.f.=8; p<0,01). For values of these parameters in the major topographical habitats refer to Table 1 (p. 20).

*Density of middens in the major topographical habitats*

By plotting the number of middens encountered at varying intervals to the transect line (Fig. 39), it was established that most, if not all, middens within 3m on either side of the transect line were detected. A total of 187 middens were detected within this fixed width transect 6m wide and 73000m long (bottom plains excluded). An overall density of 427 middens/km$^2$ of mountainous terrain is inferred.

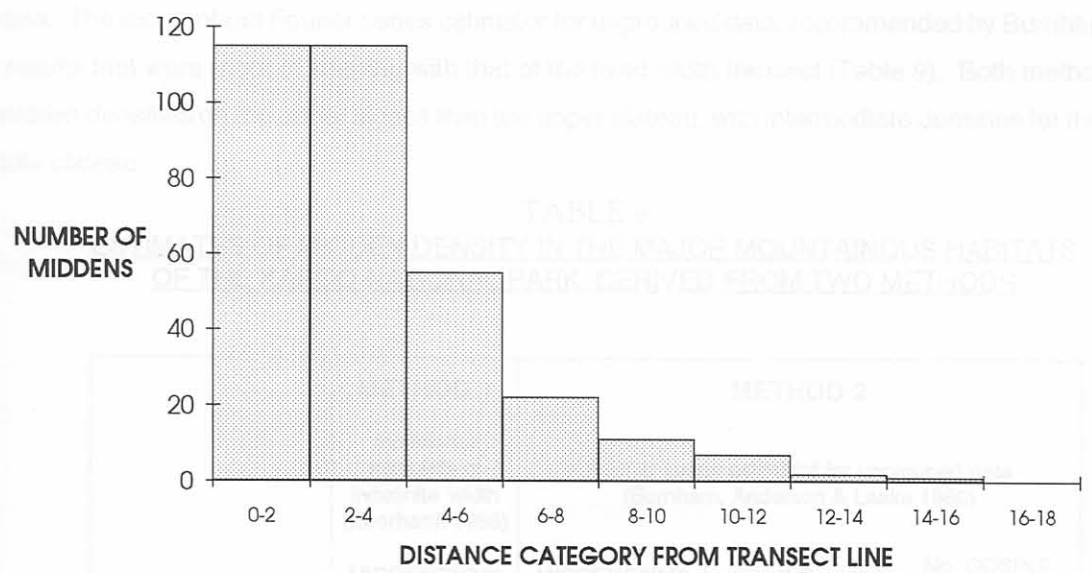



**Figure 39.** Frequency histogram showing the number of middens detected at varying distance categories from the transect line. It was assumed that all middens within 3m of the line were detected (see text).

There was no significant difference in the number of middens encountered per transect for the four mountainous habitat types. However, there was a significant difference in the mean perpendicular distances that middens were

University of Pretoria etd – Davies, R A G (1994)



TABLE 8

NUMBER OF MIDDENS ENCOUNTERED AND THEIR AVERAGE PERPENDICULAR DISTANCES FROM LINE TRANSECTS COMPLETED IN THE MAJOR TOPOGRAPHICAL HABITATS

| HABITAT | TOTAL NUMBER OF TRANSECTS | TOTAL NUMBER OF MIDDENS | MEAN PERPENDICULAR DISTANCES (m) | MEAN NUMBER OF MIDDENS PER TRANSECT |
|---|---|---|---|---|
| UPPER PLATEAU | 19 | 76 | 3,06 (sd=2,15) | 4,00 (sd=2,98) |
| UPPER SLOPES | 18 | 80 | 2,60 (sd=1,93) | 4,44 (sd=2,59) |
| MIDDLE PLATEAU | 18 | 92 | 3,94 (sd=3,21) | 5,17 (sd=4,05) |
| LOWER SLOPES | 18 | 79 | 3,24 (sd=2,35) | 4,39 (sd=3,47) |
| BOTTOM PLAINS | 4 | 0 | - | - |
| TOTAL | 77 | 327 | | |
| 1-WAY ANOVA ON MOUNTAINOUS HABITATS (bottom plains excluded) | | | F=4,30<br>p<0,01 | F=0,40<br>p>0,10 |

detected from the transect line for the different mountainous habitats (Table 8). In particular, most middens were detected close to the transect line on the upper slopes, especially when compared with those encountered on the middle plateau.

Eberhardt's (1968) model for transects of indefinite width yielded very high estimates of midden density in the major habitats when compared with the fixed-width transect (Table 9). Furthermore, the fit of the probability of detection curve to the raw data was only close for one habitat, the lower slopes, and was not statistically significant for the upper slopes data. The more robust Fourier series estimator for ungrouped data, recommended by Burnham *et al.* (1980) yielded results that were more in keeping with that of the fixed width transect (Table 9). Both methods suggested higher midden densities on the upper slopes than the upper plateau, with intermediate densities for the lower slopes and middle plateau.

TABLE 9

ESTIMATES OF MIDDEN DENSITY IN THE MAJOR MOUNTAINOUS HABITATS OF THE KAROO NATIONAL PARK, DERIVED FROM TWO METHODS

| | METHOD 1 | METHOD 2 | | |
|---|---|---|---|---|
| | models for transects of indefinite width (Eberhardt 1968) | Fourier series estimator for ungrouped data (Burnham, Anderson & Laake 1980) | | |
| HABITAT | MIDDENS/KM2 | MIDDENS/KM2 | S.E. | No. COSINE TERMS |
| UPPER PLATEAU | 417,3 | 401,9 | 55,4 | 2 |
| UPPER SLOPES | 651,3 | 552,7 | 79,4 | 3 |
| MIDDLE PLATEAU | 524,1 | 474,8 | 73,3 | 3 |
| LOWER SLOPES | 471,7 | 415,6 | 58,1 | 2 |

University of Pretoria etd – Davies, R A G (1994)



*Smaller-scale habitat preference*

There was no significant association between midden density and altitude. However, midden density did vary with orientation. Within the lower slopes habitat type, there was a statistically significant difference in the number of middens encountered per transect between slopes of varying aspect (Kruskal Wallis 1-way anova: $X^2$=9,2; d.o.f.=3; p<0,05). Particularly low numbers of middens were encountered along transects on northerly aspects (mean=0,4; n=5). High numbers of middens were encountered along transects on southerly (mean=6,8; n=4) and westerly (mean=5,8; n=6) aspects. The same trend was apparent within the upper slopes habitat type, but small samples of especially northerly aspects (n=1) precluded any tests.

There was a tendency for more middens to be encountered along transects running across gentle slopes (mean=5,3; n=13) than along transects running across steep slopes (mean=3,9; n=23). This tendency was not statistically significant. However, a $X^2$ contingency table comparing observed frequencies of middens for the various slope ratings with expected frequencies (as derived from the microhabitat assessment loci) revealed a statistically significant association between middens and slope rating ($X^2$=7,9; d.o.f.=2; p<0,05). As indicated previously, middens were positively associated with gentle slopes and negatively associated with steep slopes. Flat areas appeared to be used roughly in proportion to their availability.

There was no evidence that local plant cover or the density of large shrubs might influence the distribution of middens. However, midden loci had higher average bush:grass ratios (more shrubby) than microhabitat assessment loci when compared for each transect. This difference was statistically highly significant (t-test for matched pairs: t=3,27; p<0,01).

Middens on the lower slopes occurred significantly closer to episodic water courses than expected from the microhabitat assessment loci (unequal variances t-test: t=2,53; d.o.f.=130,5; p<0,05). No such differences were obtained for the middle plateau or upper slopes. By contrast, middens on the upper plateau occurred significantly farther from the water courses than expected from the microhabitat assessment loci (equal variances t-test: t=-2,63; d.o.f.=167; p<0,01).

Midden loci on plateaus occurred closer to substantial rock outcrops (mean=39,5m; s.d.=73,3; n=168), than expected from microhabitat assessment loci (mean=74,2m; s.d.=135,0; n=185). This difference was statistically highly significant (unequal variances t-test: t=3,04; d.o.f.=289,3; p<0,01). There was no evidence for association between midden loci and substantial rock outcrops on either of the slope habitats.

The observed frequencies of the various rock categories associated with midden loci were compared with their expected frequencies derived from the microhabitat assessment loci. On the plateaus there was a statistically highly significant association between middens and certain rock types ($X^2$=63,6; d.o.f.=4; p<0,01). In particular, middens were negatively associated with non-rocky areas and positively associated with large loose rocks and boulders (as an aggregated category). On the slopes, where non-rocky areas are negligible (Table 1, page 20), middens were positively associated with small loose rocks at the expense of all larger outcrops ($X^2$=16,1; d.o.f.=3; p<0,01).

University of Pretoria etd – Davies, R A G (1994)



*Distribution of middens at Mountain View*

The 56 middens located in the rocky 12,3ha study area at Mountain View represent a density of 455 middens/km$^2$ which is compatible with those estimates given previously. Analysis of the nearest-neighbour distances between these middens yielded a G-value of 0,67 indicating a dispersion pattern that was borderline between regular and random.

*Faecal accumulation rate*

Eleven collections of faecal pellets were made from the Mountain View middens spanning the three sampling periods. The first collection in each sampling period was excluded from analyses because of ambiguity in the classification of fresh (<2 days old) faecal pellets. A total of 9223 fresh pellets were collected during the remaining eight samples which represent the accumulations of 463 midden nights. A nightly accumulation rate of 19,9 faecal pellets per midden is inferred. The accumulation of pellets varied widely between middens and also between collection dates. No faecal pellets were found outside of middens despite searching.

Although collections of fresh faecal pellets from middens within the Mountain View study area were generally smaller than those collected elsewhere (n=63), we could detect no significant differences between the study area and other habitats in this regard.

*Recovery of faecal pellets marked with fluorescent pigments*

The first captured rabbit treated with fluorescent pigment received high dosages of the pigment over an extended capture period. After release of this rabbit a total of 201 marked faecal pellets were detected, distributed over eight middens up to six nights after release. The second and third captured rabbits received single doses of pigment and were released immediately. Fewer marked faecal pellets were detected from these rabbits (totals=107 and 81). These pellets were distributed over three middens each and were collected up to four nights after release for both individuals.

*Energy content of faecal pellets*

Faecal pellets collected during July were heavier (mean mass=0,238g; s.d.=0,025; n=100) than those collected during January (mean mass=0,207g; s.d.=0,037; n=80). This difference was statistically significant (Mann-Whitney U test: z=2,18; p<0,05). Mean mass (dry weight) for all pellets weighed was 0,223g. Energy content of pellets was very similar for the two periods: ten pellets assessed in January had an average energy content of 19,05KJ/g (s.d.=0,32); ten pellets assessed in July had an average energy content of 19,08KJ/g (s.d.=0,51). An average faecal pellet contains 4,25 kilojoules of energy.

University of Pretoria etd – Davies, R A G (1994)



# DISCUSSION AND POPULATION ESTIMATE

*Middens as indicators of habitat preference*

Most census methods employed concurred that red rock rabbit middens occur at densities of about 400-500 $km^{-2}$ in the rocky, mountainous habitats of the Karoo National Park. Little faith can be placed in the excessive density estimates derived from Eberhardt's (1968) model for transects of indefinite width, as this model did not adequately describe the probability of detection curve. The robust Fourier Series estimator provided estimates of density (with reasonable standard errors) that were more compatible with density estimates derived from the fixed width transect and the mapping of middens at Mountain View.

Although encounter rates for middens were not significantly greater per transect in the upper slopes habitat, greater densities in this habitat can be inferred from perpendicular distance data which indicate lower detectability of middens in this more difficult terrain. Both models for density estimation presented the same order of habitat preference: upper slopes > middle plateau > lower slopes > upper plateau. Preference for upper slopes over lower slopes might be due to generally taller vegetation, better distribution of boulder outcrops and the absence of northerly aspects. Comparable densities might have been found for lower slopes if northerly aspects had been excluded. Such high densities on slopes are probably permitted by a close dispersion of large rock outcrops and the near absence of non-rocky areas. Preference of the middle plateau over the upper plateau as indicated by midden density is probably due to a large proportion of unsuitable (non-rocky) terrain in the latter habitat type.

Despite documented accounts of a dietary preference for grasses by *Pronolagus* spp. (Stewart 1971; Peddie 1975), this study showed that middens occurred at significantly lower density in very grassy areas. Some shrubs may be required to provide shade and cover for resting rabbits. But north-facing aspects tend to be the most grassy areas, and these slopes may simply be too hot during the day to offer comfortable resting spots. Thermoregulatory constraints have been shown to influence the dispersion of other small mammals such as the Alpine marmot (Turk & Arnold 1988).

Gentle slopes were the favoured gradient in this study. Widely-dispersed loose rocks on gentle slopes probably afford ideal escape routes for red rock rabbits, and indeed middens were positively associated with this rock category. The less rocky flat areas (plains and plateaus) were neither preferred nor avoided overall. Steep slopes were avoided, possibly because this habitat encompasses difficult terrain, with bare screes covering wide areas.

The observed relationship between the distribution of middens and that of episodic water courses is obscure. Avoidance of water courses on the upper plateau may be a consequence of the fact that most water courses in this habitat are situated in non-rocky, small valleys (unlike all other habitats). Water courses on the lower slopes, by contrast, descend through gulleys which afford shelter amongst rocks and riparian thicket. Rabbits might also be attracted to such thickets on the lower slopes for moisture in the vegetation. There was no evidence that middens were aggregated around water courses on the more mesic upper slopes.

University of Pretoria etd – Davies, R A G (1994)



The low frequencies of middens and microhabitat assessment loci encountered on large substantial rock outcrops did not indicate that these features were significantly preferred. However, middens were definitely aggregated around such outcrops in the plateau habitats. This is probably due to these features being in short supply on the flat areas. Rabbits inhabiting the mountain slopes are probably never far from such outcrops, especially on the boulder-strewn upper slopes. It seems likely that the rabbits require access to these features within their ranges.

Large rock outcrops are probably important to red rock rabbits for the refuges they provide in rock crevices. The observation that red rock rabbits can also lie up in forms amongst the vegetation suggests that rock crevices are required as shelter from predators rather than from the elements. Availability of such refuge might be more critical for the survival of juvenile rabbits than adults. Although *Pronolagus* spp. are recorded to nest amongst dense vegetation (Skinner & Smithers 1990; Pepler 1990), it seems likely that interstices under or between rocks would be used by red rock rabbits in the less vegetated Karoo. Indeed two juvenile rabbits, when flushed, were observed to find sanctuary in holes under small boulders (pers. obs.).

*Middens as indicators of rabbit abundance*

The present conversion of estimates of midden density into estimates of rabbit abundance using faecal accumulation on middens is based on two preliminary assumptions that require justification. First, it is assumed that all faecal pellets are deposited on middens. Secondly, it is assumed that faecal accumulation rate in the Mountain View study area is representative of all habitats in the park.

Wild rabbits *Oryctolagus cuniculus* also use middens or 'dung-hills' for territorial purposes, and it has been shown that only a proportion of faecal pellets are deposited on these dung-hills (Mykytowycz & Gambale 1969). However, *O. cuniculus* (unlike *P. rupestris*) is a social species and use of middens in this species serves to define boundaries between groups, and varies with the social status of the individual (Cowan 1987). Middens of red rock rabbits are large, more frequent and appear to be more regularly spaced. In justification of the first assumption, no faecal pellets were found away from middens, even when searching with ultra-violet light to illuminate pellets marked with fluorescent pigment at night.

The absence of a significant difference between fresh faecal accumulations on middens in the various habitats is considered to be justification for the second assumption. The tendency for larger samples to be collected on middens outside the Mountain View study area is probably due to these being first collections - when separation of fresh pellets is more ambiguous.

Recovery of faecal pellets marked by fluorescent pigment from treated rabbits was disappointing. It appeared that the pigments were voided from the rabbits' digestive tracts too rapidly for meaningful evaluation of defecation rate and the number of middens visited. Some pellets were evidently overlooked on the first collection after release and picked up in later collections. But recovery of marked faecal pellets did indicate that daily defecation rate probably exceeds 150 pellets and that single animals range over at least 3-8 middens.

University of Pretoria etd – Davies, R A G (1994)



Although the deposition of faecal pellets on middens at Mountain View appeared highly variable, regular clearing of a large number of middens should have yielded a reliable estimate of average faecal accumulation rate per midden per night (19,9 pellets). Peddie (1975) reported that a captive *P. randensis* produced approximately 21g of faecal pellets per day (dry weight). This would correspond to 94 faecal pellets using our data which would indicate a ratio of approximately 4,7 middens per rabbit. However, the captive animal was a juvenile and was fed a high quality diet.

*Oryctolagus cuniculus* can produce up to 820 faecal pellets per day (Taylor & Williams 1956). The literature suggests lower defecation rates for other leporids: *Lepus timidus timidus* produced 200-450 faecal pellets per day (Lampio 1952); while *Lepus timidus scoticus* produced 208 (33-450) faecal pellets per day (Flux 1970). If red rock rabbits produce about 250 pellets per night, a ratio of 12,6 middens per animal is inferred.

The energy content of winter and summer faecal pellets was very similar but larger pellets were collected during winter. This might be due to a higher proportion of juveniles in the population during summer, or to rabbits consuming greater quantities of bulk food during winter.

The digestive efficiency of most leporids is about 50% (Slade & Hintz 1969; Holter, Tyler & Walski 1974; Mautz, Walski & Urban 1976; Walski & Mautz 1977). Therefore, 85KJ of faecal energy accumulating on the average midden each night can be taken to represent roughly 85KJ of energy digested, and 72KJ metabolised (80-90% of digested energy is usually metabolised by leporids: Walski & Mautz 1977). The field metabolic rate of a red rock rabbit weighing 1,62kg (mean mass given by Skinner & Smithers 1990) is calculated at $1280KJd^{-1}$, using Nagy's (1987) equation for eutherian herbivores. This is close to values estimated for black-tailed jackrabbits *Lepus californicus* of comparable mass (Shoemaker, Nagy & Costa 1976; French & Heasley 1981). It can be concluded that faecal energy accumulating on 17,8 middens represents sufficient energy metabolised to fulfil the requirements of a single adult rabbit. Actual ratio of middens per animal would be lower than this because a proportion of the population is comprised of juveniles with lower total metabolic requirements. Considering faecal production and accumulation rates (above) as well, the ratio of middens per animal probably lies between 13 and 18. It is concluded that a relationship of 15 middens to a single rabbit is realistic.

Estimates of rabbit abundance in the topographical habitats and the Karoo National Park using this ratio are given in Table 10. Midden density in the mountainous terrain of the park probably corresponds to an overall density of 30 rabbits/$km^2$, and biomass levels of about 45kg/$km^2$ (using a mean mass of 1,5kg). Density of *P. randensis* was estimated to be far higher (265 rabbits/$km^2$ of koppie habitat) in the wetter Matobo Hills National Park in Zimbabwe (Peddie 1975). The population size estimated for red rock rabbits in the Karoo National Park (n=6652) is approximately half that estimated for rock hyrax in the park (n=13335). Red rock rabbits are approximately twice as abundant on the rocky plateaus as rock hyrax, but the latter outnumber red rock rabbits by a factor of three on the mountain slopes (Table 4, page 48). Together these two small herbivores comprise the major component of the park's herbivore biomass, especially in the rocky areas. It should be noted that red rock rabbit numbers appear to be highly variable: there was a ten-fold difference in the number of rabbits encountered in 1987 and in 1989 (see Fig. 40b, p. 81).

University of Pretoria etd – Davies, R A G (1994)



TABLE 10

POPULATION ESTIMATE FOR RED ROCK RABBITS IN THE VARIOUS MAJOR HABITATS OF THE KAROO NATIONAL PARK

The extent of the park in this analysis was as described in Chapter 2. Surface areas for the respective habitats were determined by use of an image analyser and were compensated for gradient on the lower slopes (increased by 5,8%) and on the upper slopes (increased by 9,6%). Midden densities were derived using the Fourier Series Estimator (see text). An average ratio of 15 middens per rabbit was used to predict rabbit numbers (see text).

| HABITAT | SURFACE AREA (km2) | MIDDEN DENSITY (No./km2) | NUMBER OF MIDDENS | NUMBER OF RABBITS | RABBIT DENSITY (No./km2) |
|---|---|---|---|---|---|
| UPPER PLATEAU | 33,8 | 401,9 | 13596 | 906 | 26,8 |
| UPPER SLOPES | 42,1 | 552,7 | 23263 | 1551 | 36,8 |
| MIDDLE PLATEAU | 62,3 | 474,8 | 29566 | 1971 | 31,7 |
| LOWER SLOPES | 80,3 | 415,6 | 33356 | 2224 | 27,7 |
| BOTTOM PLAINS | 117,1 | 0 | 0 | 0 | 0 |
| MOUNTAINOUS TERRAIN | 218,5 | 456,8 | 99781 | 6652 | 30,5 |
| ENTIRE PARK | 335,6 | 297,3 | 99781 | 6652 | 19,8 |

*Middens as indicators of territoriality*

As stated in the introduction middens or latrines are associated with a territorial function in a diverse array of mammal species. Many of these mammals have evolved different ways of depositing olfactory signals on such latrines to advertise presence in their territory. This suggests strong selective pressure for this behaviour in territorial species. *Oryctolagus cuniculus* conveys olfactory signals via strategically distributed dung-hills by coating faecal pellets with a secretion from the anal gland and by 'chinning' on proximate landmarks, and the anal glands of territorial leporids are much larger than those of even closely-related non-territorial species (Mykytowycz 1968). Enlarged anal glands in red rock rabbits would be highly suggestive that middens fulfil a territorial function. Fresh faecal pellets on red rock rabbit middens are indeed characterised by a shiny, waxy coating (pers. obs.). Aggression and chasing, which often ensue between red rock rabbits after one has been disturbed from its area, are also highly suggestive that this species is territorial (Pepler 1990, pers. comm.).

Unlike most other territorial lagomorphs however, *Pronolagus* species are solitary. Dung-piles of *O. cuniculus* are mostly maintained by dominant animals in each group, and are often clustered on the boundaries between groups (Mykytowycz & Gambale 1969; Cowan 1987). Such latrines probably help stabilise relationships between neighbouring groups as in badgers (Roper *et al.* 1986). Red rock rabbit middens were not clustered in our Mountain

University of Pretoria etd – Davies, R A G (1994)



View study area. If all faecal pellets of this species are deposited on middens, the middens need to be practically placed within each individual's range for access, but sufficiently spaced to act as strategic indicators of presence (which would require regular visits).

Why should *P. rupestris*, unlike most solitary lagomorphs (including two other species found in the KRNP), be territorial? Territories are defended areas (Noble 1939), and territorial behaviours (such as acts of defence and the exclusion of rivals from fixed areas) are usually only warranted when some resource is economically defensible (Brown 1964). Cowan & Bell (1986) point out that there is greater potential for competition amongst leporids that rely on some form of cover, and that these species are more often territorial. The pika, *Ochotona princeps*, is also a solitary and territorial lagomorph (Svendsen 1979). Like red rock rabbits, pikas do not burrow and rely on interstices amongst rocks on talus slopes for their refuge requirements. Crevices and fissures, irregularly distributed through rocky terrain, appear to comprise a critical resource that is worth defending by vulnerable small mammals in predator-rich environments (red rock rabbits were easily captured by black eagles and caracals once detected away from cover - pers. obs.). Lagomorphs have no control over this resource and must defend what is available. Escape routes to such refuge sites are probably required by adult rabbits, but the crevices might also be critical as safe nest sites for raising young.

University of Pretoria etd – Davies, R A G (1994)



# DISTRIBUTION AND ABUNDANCE OF ALTERNATE PREY

## PART 2: NOTES ON OTHER SPECIES

During the course of fieldwork, attempts were made to gather as much information as possible on other potential prey of black eagles in the KRNP, besides rock hyrax and red rock rabbits. This was done primarily to provide a framework for understanding black eagle feeding habits (Chapter 9). Besides conventional prey recorded for black eagles such as hares, game birds, small antelope (see Chapter 9), notes were kept of larger animals which may provide food to the eagles in the form of juveniles or carrion. While conducting fieldwork in the KRNP between 1986 and 1990, detailed notes were kept of the time spent in the field and locations visited. All potential prey seen were recorded, and where possible I also noted details of local habitat conditions for each sighting (using the variables as listed in Table 7, page 67). Each May (1987 onwards) the National Parks Board conducted total counts of all large ungulates in the park by helicopter (Randall *in litt.*).

A total of 567h were spent walking through the KRNP in the course of fieldwork. Most of this walking was conducted in mountainous terrain to and fro hyrax colonies and eagle nests. Prey sightings while specifically observing hyrax were excluded while calculating relative abundance of hyrax to avoid bias. A total of 1304 potential prey animals were sighted. Relative frequencies and relative biomass of the different prey species are presented in Table 11. For scientific names, consult Appendix 2.

Detailed census techniques (Chapters 4 & 5) indicated that rock hyrax outnumber red rock rabbits by a factor of two in the KRNP, yet hyrax and red rock rabbits were encountered at a ratio of 26:1 while walking in the park. This disparity reflects the cryptic and nocturnal nature of red rock rabbits, and suggests that rock hyrax should be relatively much more available to black eagles foraging at similar times and in similar places to myself.

TABLE 11

INCIDENTAL OBSERVATION OF POTENTIAL PREY SPECIES IN THE KRNP

Ungulate lambs refer to lambs of medium-sized animals e.g. springbok; mountain reedbuck and grey rhebok are not included in the frequency and biomass analysis because they are not preyed on as adults; the figure of 905 hyrax was derived from relative encounter rates when this species was not specifically being searched for (n=443h); all mass estimates from Skinner & Smithers (1990) and Maclean (1985); consult Appendix 2 for scientific names.

| SPECIES | N | % FREQUENCY | ADULT MASS (kg) | BIOMASS (kg) | % BIOMASS |
|---|---|---|---|---|---|
| rock hyrax | 905 | 69,40 | 3,20 | 2896,0 | 47,46 |
| red rock rabbits | 35 | 2,68 | 1,62 | 56,7 | 0,93 |
| Cape hares | 4 | 0,31 | 2,04 | 8,2 | 0,13 |
| scrub hares | 5 | 0,38 | 3,60 | 18,0 | 0,29 |
| steenbok | 31 | 2,38 | 11,10 | 344,1 | 5,64 |
| klipspringer | 212 | 16,26 | 11,90 | 2522,8 | 41,34 |
| grey duiker | 4 | 0,31 | 11,00 | 44,0 | 0,72 |
| large ungulate lambs | 32 | 2,45 | 5,00 | 160,0 | 2,62 |
| mountain reedbuck | 46 | - | - | - | - |
| grey rhebok | 41 | - | - | - | - |
| yellow mongoose | 1 | 0,08 | 0,83 | 0,8 | 0,01 |
| small grey mongoose | 14 | 1,07 | 0,80 | 11,2 | 0,18 |
| Cape wildcat | 2 | 0,15 | 4,30 | 8,6 | 0,14 |
| Cape fox | 2 | 0,15 | 4,10 | 8,2 | 0,13 |
| greywing francolin | 53 | 4,06 | 0,39 | 20,7 | 0,34 |
| karoo korhaan | 4 | 0,31 | 0,75 | 3,0 | 0,05 |
| SUMMARY: | | | | | |
| HYRAX | 905 | 69,40 | - | 2896,0 | 47,46 |
| LAGOMORPHS | 44 | 3,37 | - | 82,9 | 1,36 |
| SMALL ANTELOPES | 247 | 18,94 | - | 2910,9 | 47,70 |
| UNGULATE LAMBS | 32 | 2,45 | - | 160,0 | 2,62 |
| CARNIVORES | 19 | 1,46 | - | 28,8 | 0,47 |
| GAME BIRDS | 57 | 4,37 | - | 23,7 | 0,39 |
| TOTAL | 1304 | 100 | | 6102,3 | 100 |

University of Pretoria etd – Davies, R A G (1994)



Different species of lagomorphs in the park exhibited similar flushing behaviour (distances) to one another (pers. obs.), so their encounter rates should reflect relative densities. From encounter rates it appears that Cape hares *Lepus capensis* and scrub hares *Lepus saxatilis* occur at approximately one eighth of the numbers of red rock rabbits, with respective population sizes estimated at 760 and 950 (Table 12). However, much of the habitat sampled on foot was the preferred mountainous habitat of red rock rabbits - this occupies about 80% of the total park area. Cape hares prefer the short arid scrub on the plains (Table 13), and scrub hares prefer taller vegetation. These habitats were probably under-represented when walking, so the populations of these leporids may be under-estimated.

TABLE 12
POPULATION ESTIMATES FOR VARIOUS POTENTIAL PREY SPECIES IN THE KRNP
See text for methods

| SPECIES | method | ESTIMATE |
|---|---|---|
| rock hyrax | Chapter 4 | 13335 |
| red rock rabbits | Chapter 5 | 6652 |
| Cape hares | sighting ratios | 760 |
| scrub hares | sighting ratios | 950 |
| steenbok | sighting ratios | 200 |
| klipspringer | sighting ratios | 1200 |
| grey duiker | sighting ratios | 50 |
| springbok | helicopter census | 1285 |
| mountain reedbuck | helicopter census | 220 |
| grey rhebok | helicopter census | 276 |
| small grey mongoose | sighting ratios | 210 |

Numbers of most other prey species in the KRNP cannot be predicted from encounter rates because of variation in visibility and behaviour. However, some inferences may be drawn by marrying the encounter rates with the results of the helicopter censuses. Klipspringers *Oreotragus oreotragus* are likely to be overlooked by helicopter count but not by groundwork. Klipspringer were encountered roughly five times more often than mountain reedbuck *Redunca fulvorufula* or grey rhebok *Pelea capreolus* on foot. Populations of these species were reliably estimated at @250 each over the study period from the helicopter census. Relative encounter rates on the ground suggest that the KRNP may accommodate about 1200 klipspringer. Population estimates of steenbok *Raphicerus campestris* and grey duiker *Silvicapra grimmia* in Table 12 are based on their relative encounter rates in comparison with that of klipspringer. These are only intended as a rough indication of numbers, both are likely to be minimum estimates because both of their preferred habitats (bottom plains for steenbok; riparian thicket for grey duiker) were under-represented by foot-sampling.

The springbok population in the park (average 1285 individuals) can be expected to produce about 450 lambs each year on the basis of a production efficiency of 35% under cropping (Davies 1985). These lambs would only be vulnerable to black eagle attack for maybe one month in the year. Availability of other ungulate lambs may be estimated in a similar way.

The encounter rates in Table 11 suggest that rock hyrax may comprise roughly 69% of the potential prey available to black eagles, and only about 47% of the available prey biomass. It should be borne in mind though that rock hyrax are very obvious when sitting on rock outcrops but may not necessarily be available to hunting eagles. Small antelope species and the lambs of larger ungulates comprise about 21% of the number of potential prey available, but a much larger proportion (50%) of the available biomass.

University of Pretoria etd – Davies, R A G (1994)



Distribution of prey sightings between major habitats (Table 13) mainly reflects my movements but gives an indication of habitat tolerance. More frequent encounters with red rock rabbits on plateaus than on slopes is not in agreement with midden distributions (this chapter) but may reflect different flushing tendencies in the different habitats. All Cape hare sightings were on flat ground (70% bottom plains). Most scrub hares (91%) were seen on flat ground, especially in the taller vegetation of the upper plateau (64% sightings). Disparity between the distributions of these two species may relate to rainfall and vegetation cover. Scrub hares were not consistently found in riparian thicket as expected. Most carnivores were seen on the bottom plains, but most Cape wildcats and caracals (sightings and scats) were located near or on rocky outcrops, along with potential prey species such as hyrax, red rock rabbits and klipspringers (detailed analysis in Chapter 7). Nearly all (95%) klipspringer sightings were on mountain slopes. Of the game birds, karoo korhaans *Eupodotis vigorsii* frequented the bottom plains, greywing francolins *Francolinus africanus* the upper plateau. Grey duikers and steenbok were most often seen on the bottom plains, especially along episodic water courses. Grey rhebok were seen on the slopes and especially the upper plateau. Mountain reedbuck were seen lower down often along river courses on gentle, lower slopes. Most springbok (84%) were recorded on the bottom plains, but towards the end of fieldwork they appeared to be moving up into the lower slopes (perhaps from population pressure on Lammetjiesleegte).

## TABLE 13
## DISTRIBUTION OF SIGHTINGS OF POTENTIAL PREY SPECIES WITHIN THE MAJOR HABITATS OF THE KAROO NATIONAL PARK

Larger mammals (last 5 spp.) and ostriches were not sampled extensively; (*) sightings of caracal and wildcat are supplemented by locations of recognisable scats; escarpments may be combined with their respective slopes.

| SPECIES | BOTTOM PLAINS | LOWER SLOPES | LOWER ESCARPMENT | MIDDLE PLATEAU | UPPER SLOPES | UPPER ESCARPMENT | UPPER PLATEAU |
|---|---|---|---|---|---|---|---|
| rock hyrax | 15 | 155 | 172 | 11 | 7 | | 24 |
| small mammals | | 3 | 1 | 1 | | | 4 |
| red rock rabbit | | 2 | 5 | | | | 11 |
| Cape hare | 7 | | | 1 | | | 2 |
| scrub hare | 2 | | 1 | 1 | | | 7 |
| yellow mongoose | 2 | 1 | | | | | |
| small grey mongoose | 9 | 4 | | | | | |
| zorilla | | 1 | | | | | |
| Cape fox | 2 | | | | | | |
| bat-eared fox | 1 | 4 | | | | | |
| Cape wildcat (*) | | 3 | 5 | | | | |
| caracal (*) | 1 | 12 | 15 | | | | |
| vervet monkey | 1 | | | | | | |
| greywing francolin | 1 | 3 | | | | | 18 |
| karoo korhaan | 2 | | | | | | |
| ostrich | 17 | | | | | | |
| grey duiker | 4 | 3 | | | | | |
| steenbok | 47 | 6 | | 2 | | | |
| klipspringer | | 65 | 13 | 5 | 16 | | |
| grey rhebok | 1 | 6 | | | 11 | | 39 |
| mountain reedbuck | 2 | 13 | | | | | |
| springbok | 384 | 70 | | | | | 5 |
| kudu | 3 | | | | | | |
| red hartebeest | 5 | | | | | | |
| black wildebeest | 2 | | | | | | |
| gemsbok | | | | 1 | | | |
| mountain zebra | 3 | 5 | | 4 | 5 | | 5 |

University of Pretoria etd – Davies, R A G (1994)



Encounter rates with rock hyrax during fieldwork showed a decline in 1988 and in 1990 which corresponded to declines as indicated by colony counts (Chapter 4) at the start and end of those respective years (Fig. 40a). This indicates that incidental encounter rates can indeed give a real indication of change in density. The hyrax declines corresponded to rainfall patterns following an apparent 3-4y cycle (Chapter 2). Summer rainfall at the start and end of 1988 comprised the low 'trough' of this cycle (Fig. 40f). Four other species showed declines reaching a 'trough' in 1988 and subsequently recovering, these were klipspringer and steenbok (as indicated by encounter rates on the ground - Fig. 40c), and kudu and grey rhebok (as indicated by helicopter census - Fig. 40d). Helicopter counts actually suggested that klipspringers and steenbok were lowest in May 1989. Red rock rabbits and small grey mongooses also exhibited population 'troughs' but lowest numbers for these species were reached a year earlier in 1987 (Fig. 40b). It may be that populations of such smaller animals respond more rapidly to rainfall effects. Only red rock rabbits and rock hyrax showed any indication of declining in 1990 when the period of lowest rainfall followed the period of highest rainfall. The prevalence of pronounced population declines in seven species in the KRNP corresponding to rainfall patterns indicates that a dry period in 1987 - 1988 was a very real ecological event for this region. The vegetation was probably already highly stressed from a more devastating drought in the early 1980's, so relationships between vegetation and consumers may have been more responsive than usual. The figures do suggest that the cyclic rainfall pattern may be encouraging osscilations in herbivore numbers. However, population change in springbok and mountain reedbuck (as indicated by helicopter census - Fig. 40e) showed no indication of a drought-related decline. Evidence of a decline in some herbivore species and not in others is puzzling but it may be explained if the requirements of selective browsers such as kudus and steenbok were in excess of their preferred food resources; while mixed feeders such as springbok (perhaps on a lower plane of nutrition) may have had more *per capita* resources to see them through the drought.

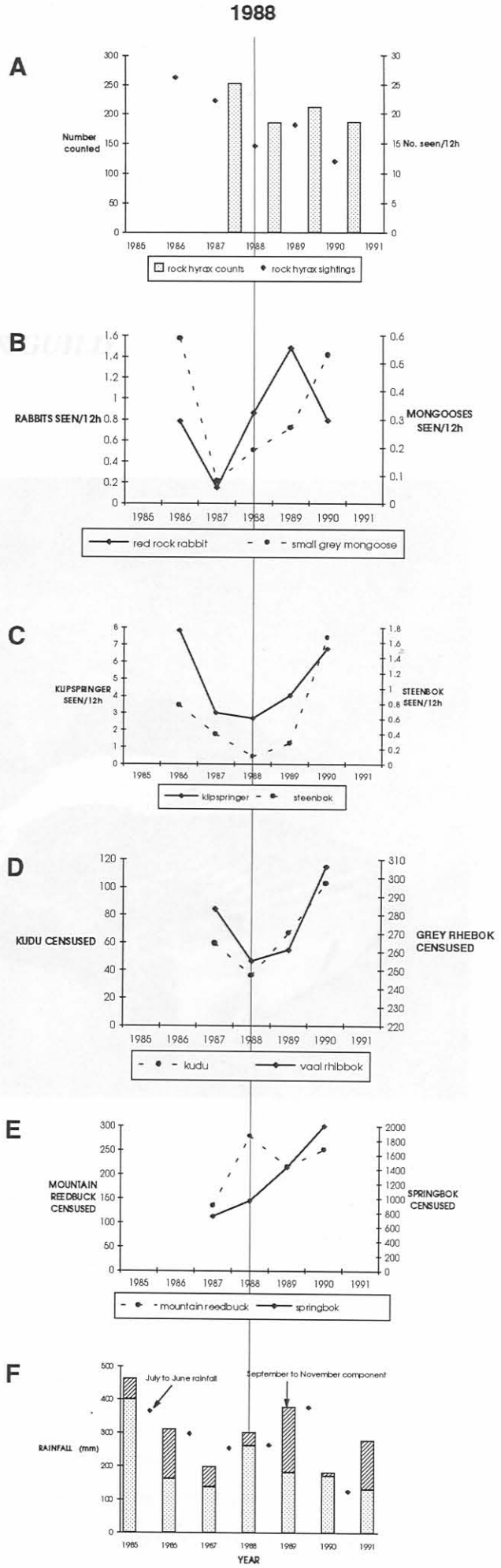
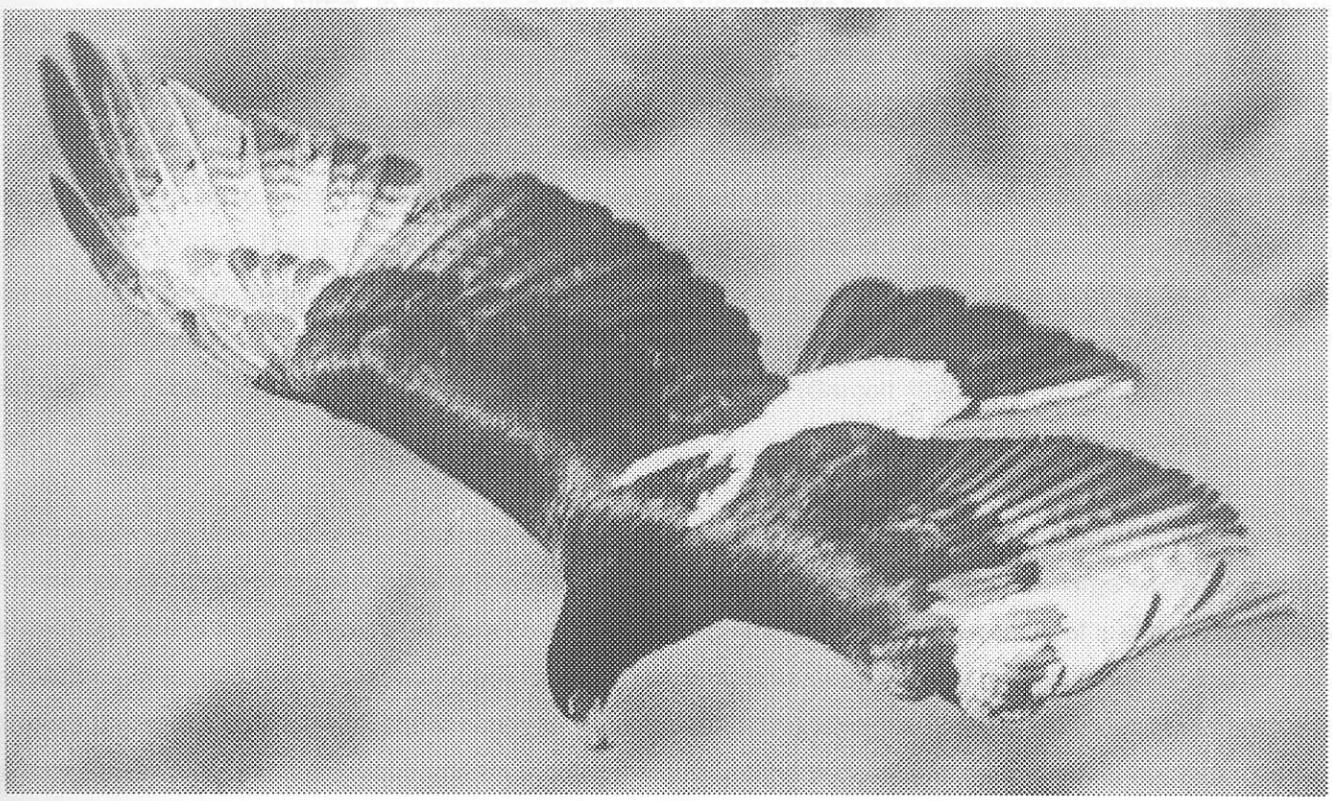



**Fig. 40.** Population change of various species in the KRNP in relation to rainfall. (D & E from Randall *in litt.* - see text for detail)

University of Pretoria etd – Davies, R A G (1994)

# *THE PREDATOR GUILD*



University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 6*

# *BLACK EAGLE DEMOGRAPHY AND BEHAVIOUR*

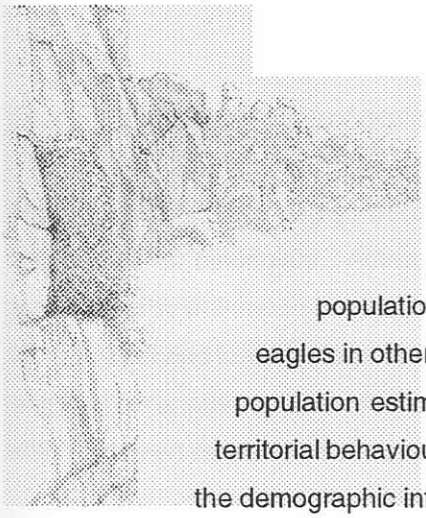
## INTRODUCTION

With a wingspan of over 2 m and weighing approximately 4 kg (Gargett 1990; pers. rec.), black eagles are very large *Aquila* eagles, second only to the golden eagle which is 14% larger by mass (A.C. Kemp *in litt.*) and occurs in the Atlas Mountains of North Africa. In all other regions of Africa black eagles are the most rapacious *Aquila*. They share the continent with two other particularly rapacious large eagles, the martial and crowned eagles, but all three are clearly separated by habitat: black eagles frequenting the mountains and rocky areas; martial eagles the plains and savannas; and crowned eagles the forests and dense bush (Brown 1976). The long wingshape of black eagles is tapered towards base and tip, and this high aspect ratio is well-suited to soaring in slope lift rather than thermals (Pennycuick 1972a). This is very evident when contrasting flight abilities of interacting black and martial eagles in mountainous terrain (pers. obs.). Black eagles are reliant on rocky habitats for nest sites on cliffs. There are very few records of black eagles nesting on other substrates such as microwave towers and electricity pylons (Boshoff & Fabricius 1986; Ledger, Hobbs & Van Rensburg 1987) and trees (Gargett 1990; C. Skinner pers. comm.; pers. rec.).

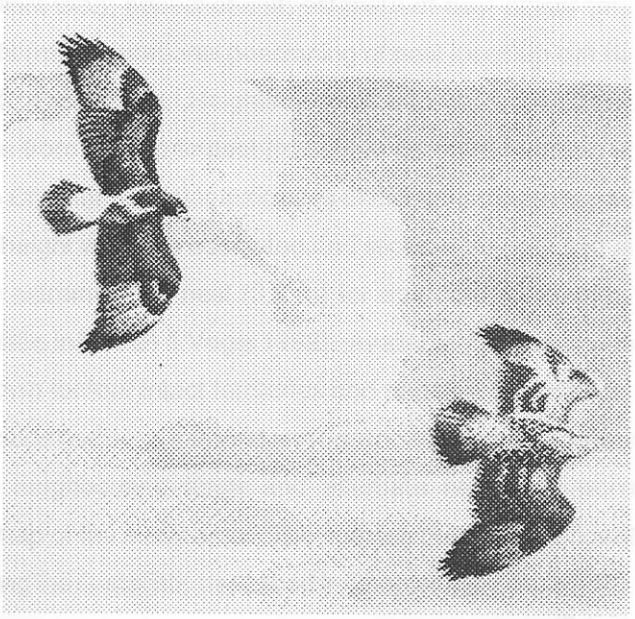
Black eagles are spectacular and conspicuous birds, and they occupy relatively small territories or home ranges. These are probably main reasons why the black eagle is one of the best-studied of all large eagles, but most knowledge of this species emanates from one in-depth, long-term and large-scale study of a particularly dense population in the Matobo Hills, led by Valerie Gargett. This project was instigated by Vernon (1965), and since then Gargett and co-workers have looked at nearly all aspects of breeding biology (especially siblicide), territoriality and spacing behaviour, diet, food requirements, feeding behaviour, time budgets and the pair-bond etc. (e.g. Gargett 1971, 1972, 1975, 1977, 1978, 1982a, 1982b, 1984). All previous aspects of the study are reviewed in Gargett (1990). Elsewhere black eagles have been the subjects for studies on breeding biology (Rowe 1947; Siegfried 1968), nest-spacing and territory/range size (Allan 1984, 1988; Boshoff & Palmer 1988; Brown 1988b), and hunting behaviour (Jenkins 1984). For more general information on black eagles see Steyn (1982) and Tarboton & Allan (1984). This extensive research has highlighted a number of unusual characteristics for this large eagle: a highly specialised diet; relatively small, well-defended territories or ranges; a very strong pair-bond; a conservative reproductive rate with obligate siblicide and a lengthy nestling period; and a breeding season which consistently occurs at much the same time of the year throughout Africa. So the preference for rock hyrax as prey by black eagles was well known, but the importance of this predation in terms of prey population dynamics had not been researched (the hyrax prey-base in the Matobo Hills is now receiving attention - Gargett 1993 unpubl.; Barry pers. comm.). The extent of livestock predation by black eagles in sheep-farming areas also warranted research. The need to cover these aspects of black eagles and their prey, together with the eminent suitability of this system for study, were prime motives for the present research (see Chapter 1).

University of Pretoria etd – Davies, R A G (1994)





To assess black eagle predation on rock hyrax in the KRNP it was essential to know how many pairs there were in the study area; whether they were territorial and excluded other eagles; over which rock outcrops, and hyrax colonies they foraged; whether they were nest-site limited; how often they raised chicks; and what factors affected this breeding rate, etc.. The present chapter provides this necessary background information on the black eagle population. The findings are contrasted with the abundant information available on black eagles in other areas, and density estimates in karoo mountain ranges are used to provide a population estimate in this region. With regard to behaviour, full details of the foraging and territorial behaviour of black eagles are provided in this chapter where they are directly relevant to the demographic influence of black eagle predation on rock hyrax. For the purposes of this thesis it was more important to know how many hyrax (and what population classes) are removed by the eagles from their ranges each year (Chapters 8 - 10) than details of when and how these hyrax are captured. However, such observations are of interest when considering the possibility of co-evolution between predator and prey, so a preliminary analysis is included here. It was also felt that these detailed observations might provide an insight as to why certain population classes of rock hyrax are more susceptible to foraging black eagles, and in such ways contribute to a better understanding of the system. Some of the more important factors affecting foraging behaviour and success are addressed, and some morphometric data are provided where these are relevant to behaviour. Further details pertaining to factors affecting prey capture rate are derived from a much larger database provided by time-lapse photography at black eagle nests in Chapter 8.



University of Pretoria etd – Davies, R A G (1994)

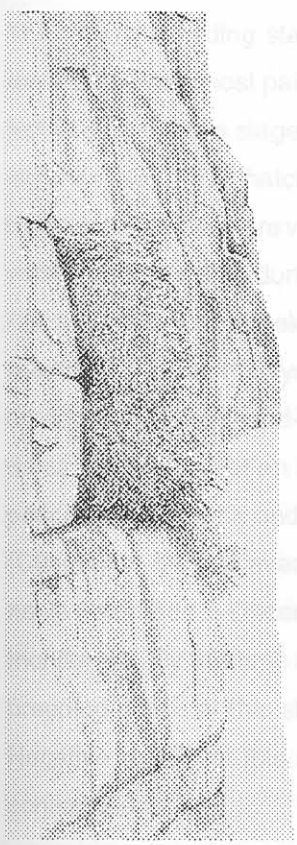


# METHODS

## *Location and identification of nesting pairs of black eagles*

Nesting pairs of black eagles were located within the study area by scrutinizing suitable cliffs with a pair of Swift Satellite 20*80 binoculars. Active nests were most obvious after the breeding season when they had become surrounded by whitewash (mutes). Location of pairs became predictable when approximate nest spacing was known for the upper and lower escarpments. Some additional unused nest sites were located during the course of habitat mapping for another part of this study (Chapter 3). By the end of the study all eagle pairs were well known and all cliffs had been carefully scrutinized for nest sites - it is unlikely that a significant number of nests were missed.

No adult resident birds were marked for this study, so productivity is given by nest-sites and their respective territories rather than by individual birds. Attempts to trap adult resident eagles with balchatris (using guinea pigs as bait) were abandoned after two weeks of intensive, unsuccessful effort. Five nestling black eagles were ringed and window-marked prior to fledging in 1987, but there were no resightings of these birds after the fledgling period, so this practice was also discontinued. For the purposes of assessing black eagle predation on rock hyrax it was not essential to be able to recognise individual eagles. It was quickly discovered that resident pairs could be identified by their behaviour, and that sexes could be distinguished on the basis of flight pattern (see later). However certain individuals were recognisable from unusual plumage characters (white feathers) and sometimes from moult patterns.



## *Nest-site selection and spacing between pairs*

To permit investigation of nest-site selection, the following parameters were recorded for each nest site: resident pair; nest number; exact locality; nest base (bush/ledge etc.); substrate of nest cliff (dolerite/sandstone/mixed etc.); substrate form (sheer cliff/pillars etc.); aspect of cliff; estimate of nest height (m); estimate of nest cliff height (m); proportional positioning of nest locus up cliff (to give height above ground); and altitude. Heights of some cliffs were measured initially, as were distances from cliff top to nest (to enable accurate focusing of time-lapse cameras - see Chapter 8). Later estimates of cliff height were based on this experience. Nest height was also estimated and sticks were collected at 0,5 m intervals from one extremely tall nest (3,6 m) for age-determination by radio-carbon analysis (details in Davies & Vogel 1992). Availability of the various types of nest cliff was known for four intact territories and parts of four adjacent territories where rock outcrops had been mapped and described in detail (Chapter 3). Distances between neighbouring nests and alternate nest sites were measured off a 1:25000 map of the study area. The spacing pattern of resident pairs was investigated using the G-statistic described in Chapter 4 (pages 39-40).

University of Pretoria etd – Davies, R A G (1994)



*Calculating population density*

A density estimate was calculated for eighteen pairs of eagles: a perimeter was drawn around the known ranges of the outermost pairs, and encompassed 435 km$^2$. The derived estimate compared favourably with that of Boshoff & Palmer (1988) for elsewhere in the Nuweveld mountains. This enabled prediction of breeding population size in these and similar mountain ranges in the Karoo. Areas encompassed by these mountain ranges were determined by superimposing a grid upon 1:500000 and 1:1000000 topographical maps of the Cape.

Inferences on the non-breeding black eagle population were drawn from knowledge of the production and fledgling periods of chicks, and from observations on the incidence of territorial intrusions. The latter were recorded during behavioural observations (see later). Intruding juveniles and subadults could all be considered as part of the non-breeding or 'floating' population. Unidentified adults however, could be either 'floaters' or neighbours. These were separated on the basis that all birds flying in pairs could be considered neighbours and that resident birds consistently spent about four minutes flying in pairs for each minute flying alone (see later). In this way, probably about 20% of unidentified intruding adults flying alone were neighbouring residents. The remainder were added to the juveniles and subadults to give some indication of the structure of the floating population. Relative density of residents to floaters was derived as the ratio of the number of times that residents were observed flying against the number of times that floaters were observed flying.

*Assessing breeding performance*

The annual breeding status of each pair was monitored by three visits during the nesting period. It was soon established that most pairs were laying eggs during June (see Fig. 44), so the first visits were timed during the first half of July - by this stage nearly all pairs making a breeding attempt should have begun incubation, although early clutches may have hatched already. Breeding status was usually assessed by viewing the nests with 20*80 binoculars, but the more viewable nests (most lower escarpment pairs) were visited to assess clutch size. Nests were visited a second time during September to monitor development of any chicks and to detect any very late breeders. Black eagle chicks develop in easily recognizable stages (Steyn 1982; Gargett 1990) and hatching dates could be predicted to within 10 days by allocating chicks to these stages. These age determinations were facilitated by drawing on experience from hand-raising a young black eagle. Laying dates (first egg) could be predicted from these hatching dates on the basis of an incubation period of 44-45 days (Steyn 1982; Gargett 1990). Some nests (9 full nestling periods) were directly and continuously monitored by time-lapse photography to provide information on feeding habits (Chapters 8 & 9), so events and the fate of hatchlings in these nests could be determined precisely. A final visit to nests was made in December each year in order to assess productivity (mean number of chicks produced per pair monitored). By this time all chicks of that year had fledged but remained in the vicinity of the nest area. Assessing breeding status at this stage was timed to coincide with collection of prey remains from beneath the nest cliffs. Negative results at this stage (disappearance of large chicks) required intensive effort and repeated visits for confirmation.

University of Pretoria etd – Davies, R A G (1994)



Correlation analyses (Ingraham *et al.* 1988) were employed to elucidate which factors may affect breeding success or failure. Annual productivity was considered in relation to rainfall and dynamics of prey populations (Chapter 4). Breeding success was considered in relation to timing of breeding, to dietary composition of the respective pairs (Chapter 9), to certain nest site parameters, and to the following characteristics of the eagle territories: total area; extent of the major topographical habitats; extent of farmland; extent of escarpment; and estimates of rock hyrax and red rock rabbit populations (derived from density estimates in the major habitats: Chapters 4 & 5). All areas were calculated by superimposing a grid over a detailed habitat map encompassing all territories. Escarpment was measured by planimeter off a 1:25000 map of the areas, and by GIS for the mapped area (Chapter 3). All statistical methods employed were carried out using the SAS computer system (Ingraham *et al.* 1988).

*Behavioural observations*

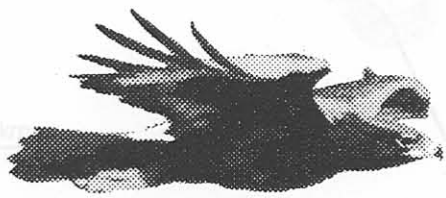
Chosen resident pairs (n=4) of black eagles were observed in stints of five continuous days (pentades). These observations were planned to evaluate the ranges of those pairs and to cover all the major periods of the year (pre-breeding, incubation, nestling, fledgling). Dawn to dusk watches were conducted from the most prominent and commanding viewpoints within each range. I did lose sight of distant flying birds on some occasions, but with practice and using the 20*80 binoculars I could track flying birds at up to seven km distance. Most pairs were not observed to travel this far from their core area, and detailed observations of the one pair that did (from different locations) suggested that this was the extreme limit of their range. Great effort was made to maintain visual contact of flying and perching eagles because they were difficult to relocate if contact was lost. For certain pairs nesting in kloofs (e.g. Kortkloof) it was impossible to view the entire range from a single location. In these cases I moved locations on different days and I also enlisted the help of observers in radio-contact (usually at the nest sites). From a sharp ridge near the Penberi nest site I had a commanding view of the entire range of this pair, and soon discovered that this was the only pair that I could keep in view almost continuously. I directed half of the total observation effort at this one pair because they yielded so much data. This pair were also clearly dimorphic (see later) permitting closer examination of the roles of the sexes. Nest sites were not always visible during these observations of foraging and territorial behaviour. Separate detailed observations were conducted at nest sites to check events on the nest against revelations of the time-lapse cameras. These observations are considered in Chapter 8.

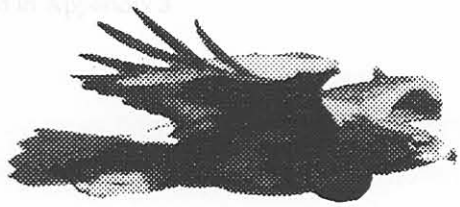
Black eagles prefer to fly where the lift is greatest at the top of a slope. They habitually skirt around escarpment and other rock outcrops, maintaining close contact with the topography at most times. During a flight I used a dictaphone to describe the route and activity of the flying birds as I watched. The only time when this technique became somewhat ambiguous was when the eagles rarely engaged in high altitude soaring flight over their ranges. In these instances I often had to wait for the birds to descend level with landmarks on the mountains before I could reconstruct their route with some confidence. Immediately after each flight, I replayed the recording and plotted the flight path either onto detailed habitat maps which I had compiled for the territory or onto transparent overlays superimposed on aerial photographs showing the topography and rock outcrops. These flight paths were then digitised onto the geographical information system compiled for the area. In the case of plots over distorted aerial photographs, reference points along escarpments and river courses were compared with the real locations of these landmarks (on the GIS) and all flight path coverages were corrected by 'rubber-sheeting' on the GIS.

University of Pretoria etd – Davies, R A G (1994)



Each flight path was given a unique ID. on the GIS to enable linking with attribute data. I recorded the following parameters for each flight: date; pair; id. (male/female/unidentified adult/pair/juvenile); time at onset; duration (measured by stopwatch in seconds where possible); origin (from perch/flight/unknown); end point (to perch/another flight/lost); primary motive (e.g. hunting, territorial display, directional flight); secondary and tertiary motives if any; ambient temperature in the shade; wind speed; wind direction; % cloud cover; % humidity; any rainfall; mean height above ground; altitude (a.s.l.); inter-mate distance; which sex led; whether the birds had full crops; which slopes they viewed; which slopes they visited; number of strikes at prey; whether they killed; and the approximate division of flying time between slow gliding flight, fast gliding flight, circling, flapping, rising in lift (unidirectional), hanging, undulating, and stooping. Distances of each flight path were later measured on the GIS and compared with respective durations to compute an overall travel speed for each flight. A database was compiled of any strikes made at prey. Unseen kills could often be inferred when the eagles were seen flying with full crops. Similar but appropriate parameters were recorded for each perching session observed, and a database was also compiled for details of each perch location (not analysed here). At regular intervals throughout each observation day important weather variables were recorded at the viewpoint. Databases were later linked on date to climatic data obtained from the automatic recording station at Beaufort West (Weather Bureau). Attributing motives to each behaviour session was complicated because perching birds could be either resting or hunting or both. Also, birds could change mid-flight from territorial display to making a strike at prey. All behavioural indications were weighed up in such circumstances (for instance perching birds were considered to be resting when seeking shelter or shade on the nest cliff, and hunting when actively choosing perches with commanding views of prey habitats).





*bulging crops indicating a feed are very noticeable on flying birds*

University of Pretoria etd – Davies, R A G (1994)



# RESULTS

Twenty three pairs of black eagles were located in and around the Karoo National Park at Beaufort West (Fig. 41). Three of these pairs are excluded from most of the following analyses either because of poor data (TG); or because the pair were seldom in occupation of their territory and never bred (MP); or because the pair occupied a different habitat outside the main study area (LX).

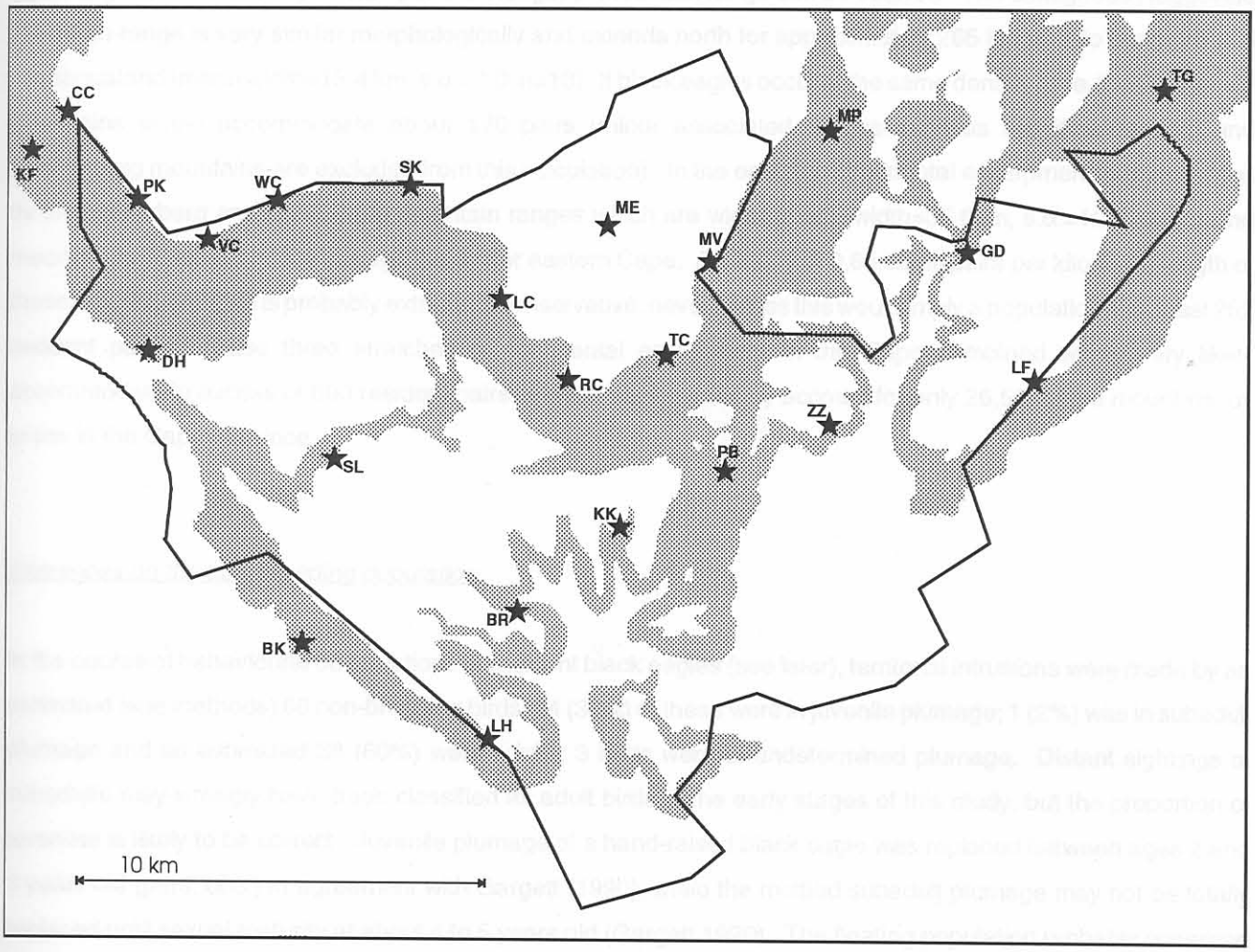



**Figure 41.** The distribution of eagle pairs resident in and around the KRNP. Symbols mark their principal nest sites. Shaded areas represent mountain slopes as opposed to plains and plateaus. Full names of each pair and their respective breeding histories are provided in Appendix 3.

## *Density of resident pairs*

Eighteen pairs, whose ranges became well known, occupied 435 $km^2$. of terrain, yielding an accurate density estimate of 4,14 pairs/100 $km^2$ for the Nuweveld mountain habitat. Black eagles are very territorial in this area - they range over all habitats with slight overlap between pairs (see behavioural observations), so an average territory size of about 24 $km^2$ can be deduced.

University of Pretoria etd – Davies, R A G (1994)



*Size of breeding population*

The Nuweveld mountain range extends for approximately 237 km through the Great Karoo at a mean width of 15,5 km (measured at 10 random localities; s.d.=3,2 km). It thus encompasses approximately 3674 $km^2$ of mountainous terrain similar to that of the study area. This mountain range probably accommodates about 152 resident pairs of black eagles, and a density of 0,64 pairs/km length of mountain range can be inferred. The contiguous Roggeveld mountain range is very similar morphologically and extends north for approximately 265 km up into the more arid Namaqualand (mean width=15,4 km; s.d.=3,0; n=10). If black eagles occur at the same density here, the Roggeveld mountains would accommodate about 170 pairs (minor associated ranges such as the Koedoesberg and Bastersberg mountains are excluded from this calculation). In the east, the continental escarpment is represented by the Sneeuberg and Winterberg mountain ranges which are wider (mean width=35,0km; s.d.=12,7; n=10) and meander for at least 410 km through the wetter eastern Cape. A density of 0,64 eagle pairs per kilometre length of these mountain ranges is probably extremely conservative, nevertheless this would imply a population of at least 262 resident pairs. These three stretches of continental escarpment in the Cape combined would very likely accommodate in excess of 600 resident pairs of black eagles yet they account for only 26,5% of the mountainous areas in the Cape Province.

*Inferences on the non-breeding population*

In the course of behavioural observations of resident black eagles (see later), territorial intrusions were made by an estimated (see methods) 66 non-breeding birds: 24 (38%) of these were in juvenile plumage; 1 (2%) was in subadult plumage and an estimated 38 (60%) were adults; 3 birds were of undetermined plumage. Distant sightings of subadults may wrongly have been classified as adult birds in the early stages of this study, but the proportion of juveniles is likely to be correct. Juvenile plumage of a hand-raised black eagle was replaced between ages 2 and 3 years old (pers. obs.) in agreement with Gargett (1990), while the mottled subadult plumage may not be totally replaced until sexual maturity at about 4 to 5 years old (Gargett 1990). The floating population probably consisted of at least 40% immature (<4,5y old) birds.

Resident black eagles made 30 times more flights over their territories than non-residents. Although subject to observer biases this flight frequency ratio gives a crude indication of relative density and suggests that there is one non-breeding bird for every fifteen resident pairs (this does not represent the black eagle population outside of breeding habitat, where non-breeders may predominate). In addition to the floating population described above, fledglings are present in 46% of territories (see later) for 3 - 4 months in each year. One can conclude that the breeding estimate of 4,14 pairs/100$km^2$ given earlier probably corresponds to an overall long-term population density of at least nine birds per 100$km^2$ within breeding habitat in the Nuweveld mountains. A total population estimate of over 1300 black eagles can be inferred for the continental escarpment areas of the Karoo, and just over 30 individuals for the KRNP.

University of Pretoria etd – Davies, R A G (1994)



*Nest spacing*

Most resident pairs of black eagles in the study area had a few alternative nest sites (range 1 - 5; mean=2,2; s.d.=1,2; n=20 pairs). Alternative nest sites varied between 0,04km and 2,39km from the most active nest of a particular pair (mean=0,49km; s.d.=0,49; n=24 distances). There was a statistically significant tendency for pairs suffering a greater amount of breeding failure to possess more alternate nest sites (r=0,46; p<0,05). This relationship prevailed despite one pair suffering very heavy nest predation being limited to only one site. There was also some indication that the number of alternate sites was related to the amount of escarpment available (r=0,39; p<0,10).

The average distance between the active nest of a particular pair and that of their closest neighbour was 2,72 km (range 1,34 - 4,51; s.d.=0,95; n=20 pairs). Analyses of these distances yielded a G-value of 0,79 which indicates that this dispersion pattern approaches regularity. However, active nests of resident pairs were spaced more widely along the lower escarpment (mean distance between sequential pairs 4,64 km; range 2,97 - 7,05; s.d.=1,47; n=11 distances) than along the upper escarpment (mean=2,71 km; range 1,49 - 4,31; s.d.=0,98; n=8 distances), see Figure 41. This difference was statistically highly significant (t-test for equal variances: t=3,23; p<0,01). The average length of escarpment encompassed by territories of upper escarpment pairs (@3,6 km) was one quarter that (@14,3 km) encompassed by territories of lower escarpment pairs.

*Nest site selection*

Most nest cliffs chosen were either dolerite cliffs (20 nests, 39%) or dolerite pillars (19 nests, 37%); eight other nests (16%) were built on sandstone cliffs; and a further four nests (8%) on cliffs of mixed substrate. With regard to nest base: four nests (8%) were sited on bushes, 43 nests (84%) were sited on cliff ledges, and another 4 nests (8%) were sited on top of dolerite pillars. One bush nest and one ledge nest disintegrated or were destroyed by baboons during the study period, both had been built on sandstone cliffs.

In the area where all rock outcrops had been mapped, there was a statistically highly significant association between nest sites and certain nest cliff substrates ($X^2$=9,21; d.o.f.=2; p=0,01). A comparison of proportional use of nest cliff substrates against proportional availability of these substrates (Figure 42) revealed that sheer dolerite cliffs were highly preferred by the nesting eagles, over dolerite pillars or sandstone cliffs.

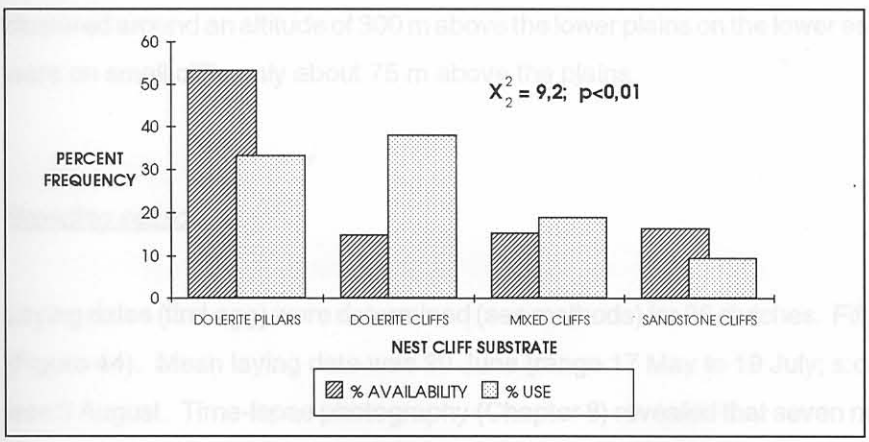



**Figure 42.** The use of different cliff substrates for nest sites, in relation to the availability of those substrates.

University of Pretoria etd – Davies, R A G (1994)



The estimated height of nests varied between 0,4 and 3,6 m (mean=1,2; s.d.=0,7; n=51). Radio carbon dating of sticks from different levels in a 3,6 m nest indicated that the material was about 14y old when brought to the nest, that the nest structure was only about 20y old, and that about 20cm of nest material is added each year (Davies & Vogel 1992). One pair (SK) attached a satellite nest to the base of a very tall nest when headroom beneath an overhang ran out. There was a slight tendency for larger nests to be found more frequently on tall cliffs (r=0,25; p=0,076).

Nesting eagles chose cliffs that ranged between 15 and 110 m high (mean=45,9; s.d.=23,4). Nests were sited on average 56,6% up these cliffs (range 15-95%; s.d.=19,7). Deduced height above ground ranged between 6 and 64m (mean=24,5; s.d.=13,0). Nests occurred proportionately higher up on small cliffs and lower down on large cliffs (r=-0,33; p<0,05), such that most nests occurred between 15 m and 40 m above the ground.

Forty nine percent of nests were sited on cliffs facing south; 27,5% faced west; 15,7% faced east; and only 7,8% faced north. Much of this pattern was no doubt due to availability of the various aspects. North-facing cliffs were the least available (12,7% of total escarpment length). But comparison of observed and expected (calculated from the extent of escarpment facing each direction) occurrences of nests revealed a statistically highly significant association between nest sitings and certain aspects ($X^2$=11,6; d.o.f.=3; p<0,01). In particular, south-facing cliffs were favoured and east-facing cliffs avoided (Figure 43).

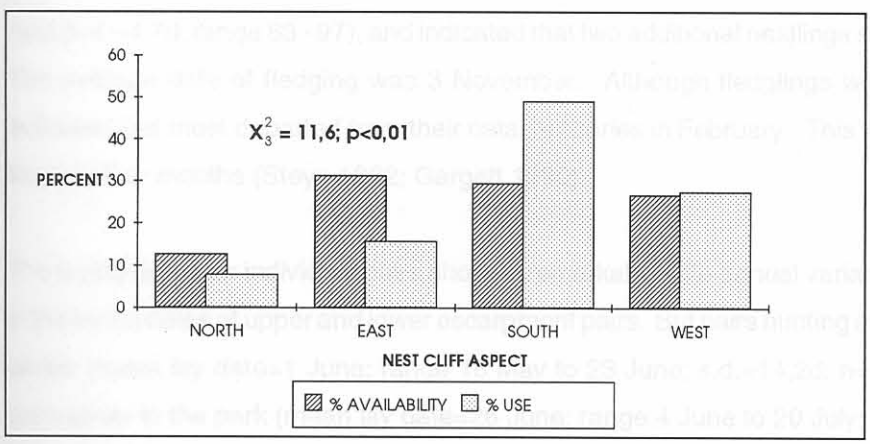



**Figure 43.** The use of different cliff aspects for nest sites, in relation to the availability of those aspects.

Thirty five percent of nests occurred on the upper escarpment cliffs, 920 m above the lower plains; 61% of nests were clustered around an altitude of 300 m above the lower plains on the lower escarpment cliffs; and a further 4% of nests were on small cliffs only about 75 m above the plains.

*Breeding season*

Laying dates (first egg) were determined (see methods) for 36 clutches. Fifty three percent of these were laid in June (Figure 44). Mean laying date was 20 June (range 17 May to 19 July; s.d.=16,8d). The average date of hatching was 3 August. Time-lapse photography (Chapter 8) revealed that seven nestlings spent an average of 88,3d in the

University of Pretoria etd – Davies, R A G (1994)



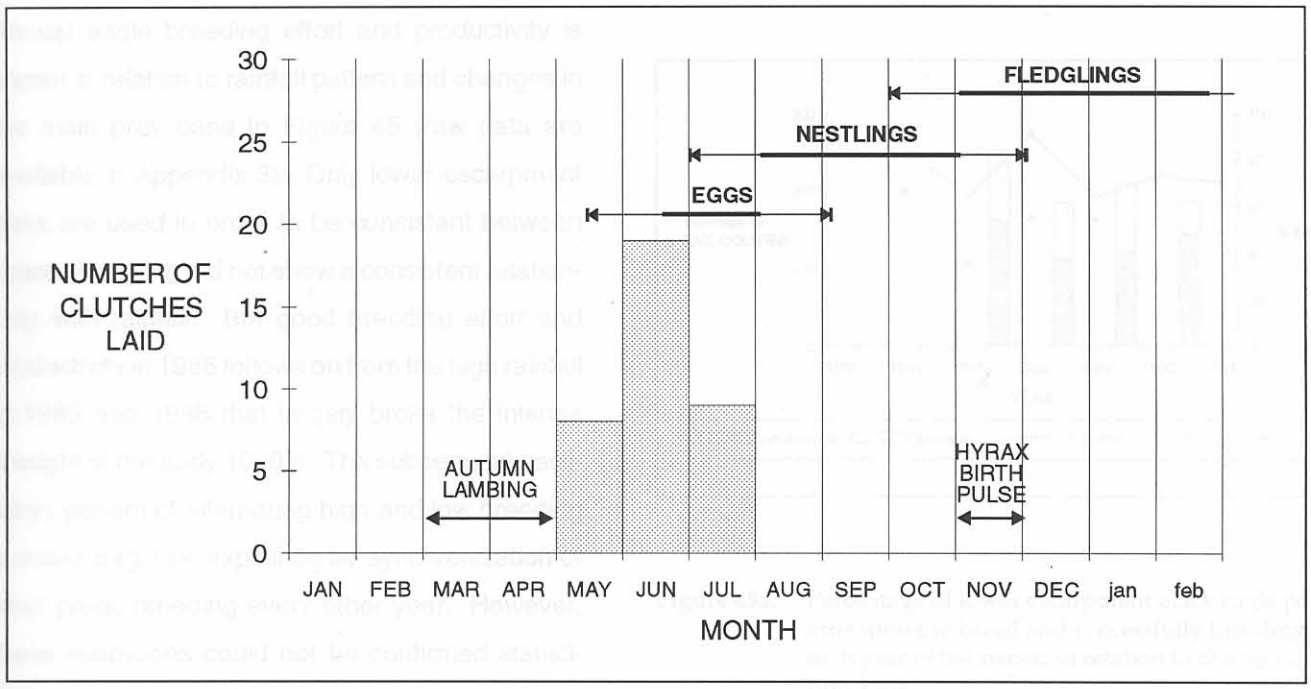



Figure 44. Breeding seasonality of black eagles in the Nuweveld Mountains during the present study. Columns represent the number of clutches laid; thick black horizontal lines represent development phases of the average chick; thin black lines represent the range of each major phase. The principal lambing season for Beaufort West farmers is shown.

nest (s.d.=4,7d; range 83 - 97), and indicated that two additional nestlings spent in excess of 81 and 88d on the nest. The average date of fledging was 3 November. Although fledglings were not closely monitored, observations indicated that most departed from their natal territories in February. This would concur with a dependent period of three to four months (Steyn 1982; Gargett 1990).

The laying dates for individual pairs showed remarkably little annual variation. There was no significant difference in the laying dates of upper and lower escarpment pairs. But pairs hunting almost exclusively on farmland (n=5) bred earlier (mean lay date=1 June; range 18 May to 23 June; s.d.=14,2d; n=10) than pairs (n=15) hunting mainly or exclusively in the park (mean lay date=26 June; range 4 June to 20 July; s.d.=10,7d; n=25). This difference was statistically highly significant (t-test for equal variances: t=6,0; p<0,01). Furthermore, pairs with more domestic bovid (sheep and goat) in their diet bred earlier (r=-0,81; p<0,01): this factor explained 65% of the variation in laying date. Farmers in the region inform me that about 65% of their lambs are born in March-April and about 35% in September.

*Breeding success*

The breeding status of established pairs became known over 84 pair years. Overall breeding effort (percentage of pairs that reached the incubation stage) was 61%. Overall productivity was 0,46 chicks/pair/year. In lower escarpment eyries I observed eight single egg clutches and 14 double egg clutches (mean=1,64; s.d.=0,49; n=22).

University of Pretoria etd – Davies, R A G (1994)



Annual eagle breeding effort and productivity is shown in relation to rainfall pattern and changes in the main prey base in Figure 45 (raw data are available in Appendix 3). Only lower escarpment pairs are used in order to be consistent between years. Breeding did not show a consistent relationship with rainfall. But good breeding effort and productivity in 1986 follows on from the high rainfall in 1985 and 1986 that largely broke the intense drought of the early 1980's. The subsequent oscillatory pattern of alternating high and low breeding success might be explained by synchronization of most pairs, breeding every other year. However, these suspicions could not be confirmed statistically. In any given pair year (including results for ten pairs monitored in 1991) there was a 65% likelihood of breeding and a 35% likelihood of not breeding. Certain pairs were consistently poor breeders. Thus the likelihood of a breeding attempt following on from a non-breeding season was low (39% likelihood; n=23). The likelihood of a breeding attempt following on from a successful breeding season was more or less as expected (68% likelihood; n=40). But more pairs tended to make a breeding attempt if the last breeding season failed (85% likelihood; n=13). In the few known instances (n=6) of pairs successfully raising chicks relatively late in the year, there was no suggestion that this led to reduced breeding effort in the following year. But early-nesting pairs did make more breeding effort (r=-0,57; p<0,05) and they were more successful (r=0,50; p<0,05).

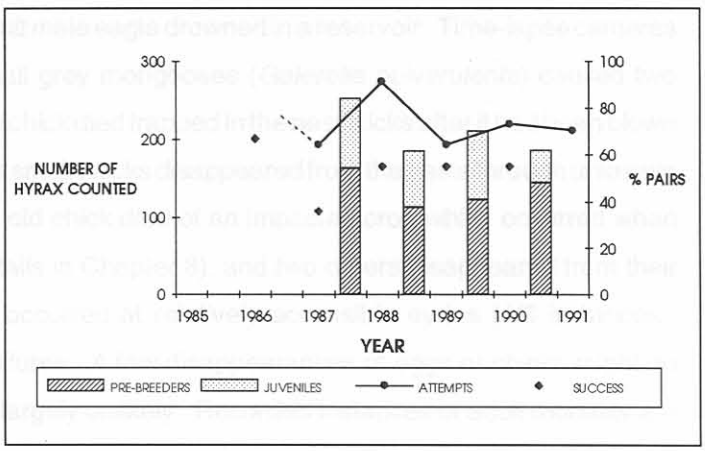



**Figure 45a.** Percentage of lower escarpment black eagle pairs attempting to breed and successfully breeding for each year of fieldwork, in relation to changes in the prey base

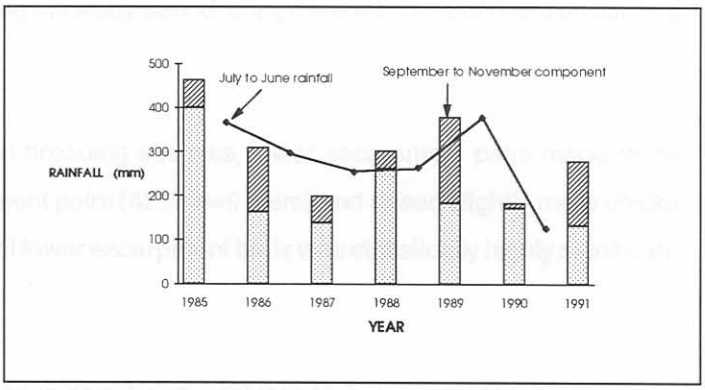



**Figure 45b.** Patterns in the rainfall recorded in the KRNP prior to, and during fieldwork.

Nineteen chicks hatched from 24 eggs that were closely monitored (79,2% viability). These eggs occurred in eight single egg clutches and eight double egg clutches. Inviability was twice as likely (4 eggs/16=25%) in double egg clutches as in single egg clutches (1 egg/8=12,5%), but only caused a breeding failure in the single egg clutch. An egg disappeared from a double egg clutch (perhaps stolen by egg-collectors), but this was not the ultimate cause of this nest failure. Siblicide occurred on all occasions (n=4) when two eggs were seen to hatch in the same nest.

University of Pretoria etd – Davies, R A G (1994)



Breeding failure occurred most often when small chicks were in the nest (6-7 out of 11 failures, see Appendix 3). In one instance a 10d old chick was abandoned when the adult male eagle drowned in a reservoir. Time-lapse cameras revealed that predation of newly-hatched chicks by small grey mongooses (*Galerella pulverulenta*) caused two consecutive failures at one eyrie, and that one two-day old chick died trapped in the nest sticks after it had been blown out of the nest bowl by gale-force winds. In other instances small chicks disappeared from the nests through unknown causes. Large chicks suffered lower mortality: one 78d old chick died of an impacted crop which occurred when feeding after an extended period without food (more details in Chapter 8), and two others disappeared from their eyries. Disappearance or predation of chicks usually occurred at relatively accessible eyries (4/6 instances). Circumstances were unknown for only two other nest failures. A few disappearances of eggs or chicks might be attributed to human depredations, but this is considered largely unlikely. Recorded instances of adult mortality are given in Appendix 3.

A link between nest failure and nest site accessibility could be demonstrated by comparing nest sites where failures occurred (n=11) with nest sites that consistently succeeded (n=15). Unsuccessful nests tended to be smaller and closer to the ground than successful nests. Nest cliffs where nest failures occurred were significantly smaller (mean height=35,8m; s.d.=15,8) than nest cliffs (mean height=55,9m; s.d.=26,3) where successful nests were sited (equal variances t-test: t=-2,3; p<0,05). Nest failure was not apparently linked with other nest site characteristics such as position on cliff or aspect, but did appear to be influenced in part by the substrate of the nest cliff. As much as 75% of nests on sandstone cliffs experienced some failure during the study period, compared with 37% of nests on dolerite and 33% of nests on mixed substrate cliffs.

With regard to the influence of habitat characteristics on breeding success, lower escarpment pairs made more breeding attempts (73%; n=11 pairs) than upper escarpment pairs (42%; n=9 pairs) and raised slightly more chicks (0,53 vs 0,35 chicks/pr/y). The enhanced breeding effort of lower escarpment birds was statistically highly significant (Kruskal-Wallis test: $X^2$=7,2; d.o.f.=1; p<0,01).

Various characteristics of the eagles' territories were used in correlation analyses to explain variation in breeding effort and success by the eagle pairs. Correlation models incorporating seven of the territory variables explained up to 83% of the variation in breeding effort but not more than 51% of the variation in breeding success, the latter being influenced by the somewhat stochastic effect of nest failure. Greater breeding effort was made in territories which were larger (r=0,69; p<0,01), had a greater extent of bottom plains (r=0,69; p<0,01), a greater extent of lower slopes (r=0,60; p<0,05), a greater extent of farmland (r=0,50; p<0,05), and a smaller extent of upper plateau (r=-0,58; p<0,01). The extent of the other major habitats did not appear to be involved with breeding effort.

Eagle pairs were divided into those (n=5) whose territories encompassed predominantly farmland, and those (n=16) whose territories encompassed predominantly parkland. Farm birds (20 pair years) showed an overall breeding effort of 85%, an overall productivity of 0,70 chicks/pr/yr, and a failure rate of 18%. Park birds (69 pair years) by contrast, showed an overall breeding effort of 59%, an overall productivity of 0,43 chicks/pr/yr, and a failure rate of 27%. These differences could not be demonstrated to be statistically significant, but the data were not well suited for statistical comparison.

University of Pretoria etd – Davies, R A G (1994)



Breeding effort was not greater in territories containing more red rock rabbits, but it was greater in territories containing more rock hyrax (r=0,49; p<0,05; prey population sizes estimated from data in Chapters 4 & 5). Comparison of breeding record and dietary parameters for the different pairs revealed no significant relationship between breeding effort and the number of species taken, or the proportion of red rock rabbits or domestic lambs in the diet. But pairs with a greater proportion of rock hyrax in their diet did make a significantly greater breeding effort (r=0,59; p<0,05). This was also the only variable which indicated some correlation with breeding success (r=0,45; p=0,07).

## *Behaviour*

### *Time budgets and activity rhythms*

During 30d observation outside the incubation period at least one member of each observation pair was in sight for 40% of the time. Coverage for the Penberi pair was much greater than this. Outside incubation, eagles spent 24,3% of their time flying and 75,7% of their time perched. When flying, individuals spent 85,4% of their time in tandem and 14,6% of their time solo. When perched, individuals spent 75% of their time together and 25% of their time apart. During incubation (10d obs.), the pair obviously spent more time perched/incubating and more time apart. Slow gliding flight and circling flight comprised most time in the air. Energetically costly flapping flight was minimised to just under 2% of flight time (Figure 46). Hunting activity occurred in three major peaks during the day separated by 3,5-4h intervals: at 08h30, 12h00 and 16h00 (Figure 47). Most flying occurred after mid morning and this was dependent on flying conditions. On very still days, smaller eagles such as booted eagles could get airborne on thermals at about 09h00, but black eagles usually began soaring two hours later than this. More supportive flying conditions may explain why most non-hunting flights by black eagles were initiated around midday and early afternoon (Fig. 47). Eagles would often indulge in territorial displays around midday.

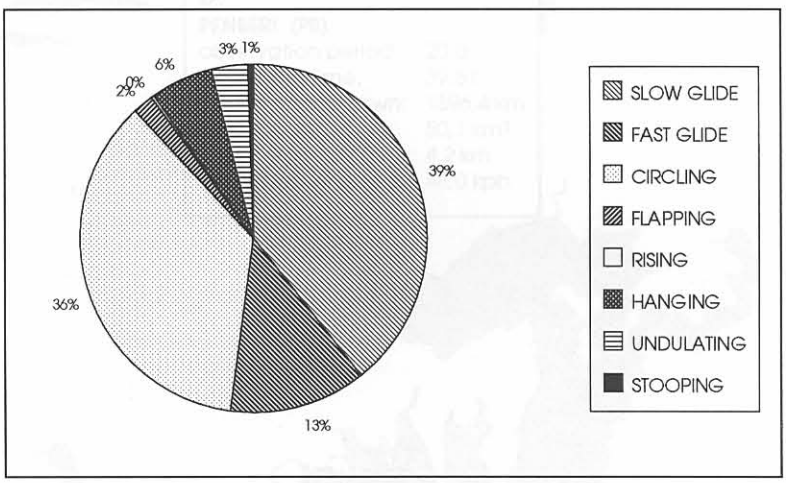



**Figure 46.** Relative duration of different flight styles used by black eagles.

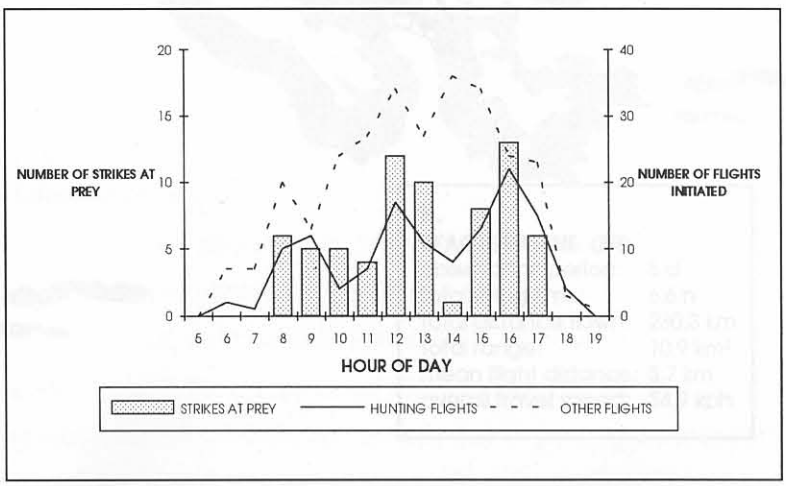



**Figure 47.** Overall daily activity rhythm of black eagles.

University of Pretoria etd – Davies, R A G (1994)



*Use of habitats*

During the full 40d of observation of four neighbouring black eagle pairs 693 flights were observed and recorded. These flight paths are shown for the separate pairs in Figure 48 along with various flight statistics. It is evident that most flying occurred over the mountain slopes and especially along the escarpment, but it should be noted that pairs with access to bottom plains (e.g. PB and LH) made extensive use of this habitat, while other pairs (BR & KK), which do not have access to the plains, appeared to be sandwiched into their smaller mountainous ranges by neighbours.

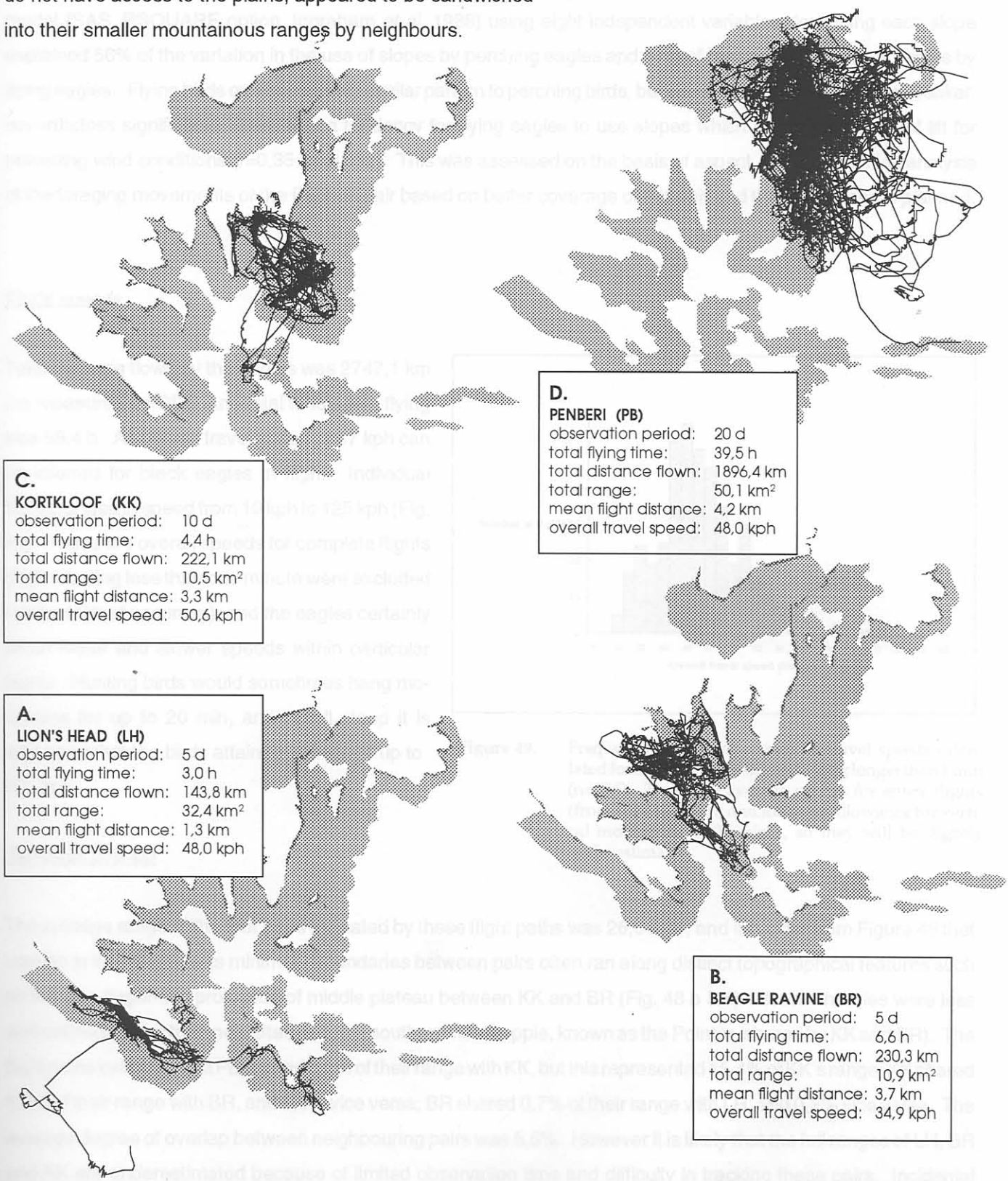



**Figure 48.** Flight paths of four adjacent pairs of black eagles in the KRNP shown against mountain slopes (grey) and escarpment (dark grey).

University of Pretoria etd – Davies, R A G (1994)



A preliminary correlation analysis on the use of slopes (no. times visited/viewed) by the Kortkloof pair revealed that perched birds made more use of slopes within their range that were more boulder-strewn ($r=0,63$; $p<0,01$), had more white-wash streaks on the rocks indicating hyrax presence ($r=0,48$; $p<0,01$), had more escarpment ($r=0,47$; $p<0,01$), were closer to the nest ($r=-0,41$; $p<0,05$), and had more ideal sandstone outcrops for hyrax ($r=0,38$; $p<0,05$). Use of slopes did not correlate significantly with area of slope, number or density of rock crevices, number or density of hyrax as predicted by an early method (see Chapter 4), nor any other quantity of refuge micro-habitats. A correlation model (SAS, RSQUARE option, Ingraham *et al.* 1988) using eight independent variables describing each slope explained 56% of the variation in the use of slopes by perching eagles and 47% of the variation in use of slopes by flying eagles. Flying birds exhibited a very similar pattern to perching birds, but correlations were somewhat weaker, nevertheless significant. There was a tendency for flying eagles to use slopes which had a high index of lift for prevailing wind conditions ($r=0,35$; $p=0,052$). This was assessed on the basis of aspect. A more detailed analysis of the foraging movements of the Penberi pair based on better coverage of this pair and their prey base is planned.

*Flight speeds*

Total distance flown by the eagles was 2747,1 km (as measured by GIS), and total time spent flying was 58,4 h. An overall travel speed of 47 kph can be inferred for black eagles in flight. Individual flights ranged in speed from 10 kph to 125 kph (Fig. 49). These are overall speeds for complete flights (flights lasting less than one minute were excluded for the sake of accuracy), and the eagles certainly attain faster and slower speeds within particular flights. Hunting birds would sometimes hang motionless for up to 20 min, and in full stoop it is estimated that the birds attained speeds of up to 200 kph.

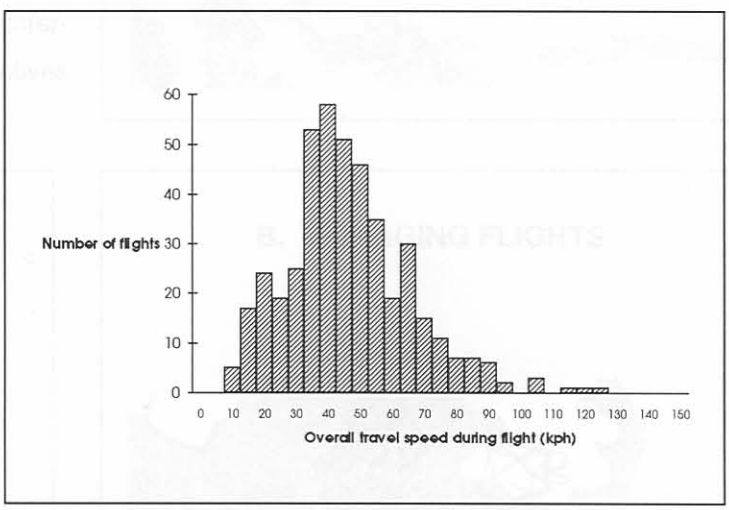



**Figure 49.** Frequency histogram of overall travel speeds calculated for all black eagle flights lasting longer than 1 min (n=826). These are average speeds for entire flights (from start to finish) and make no allowance for vertical movement of the birds, so they will be slightly underestimated.

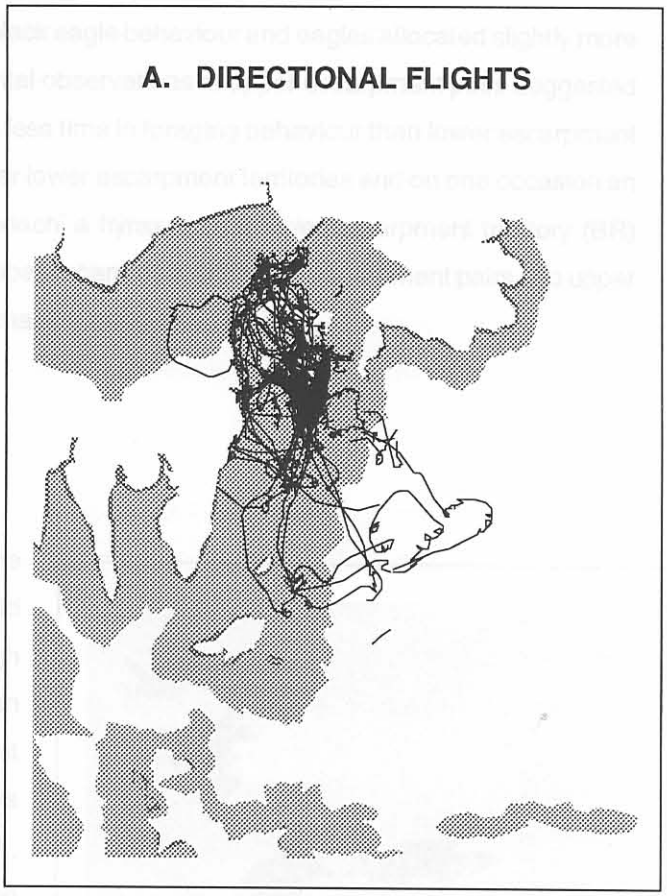
*Territorial overlap*

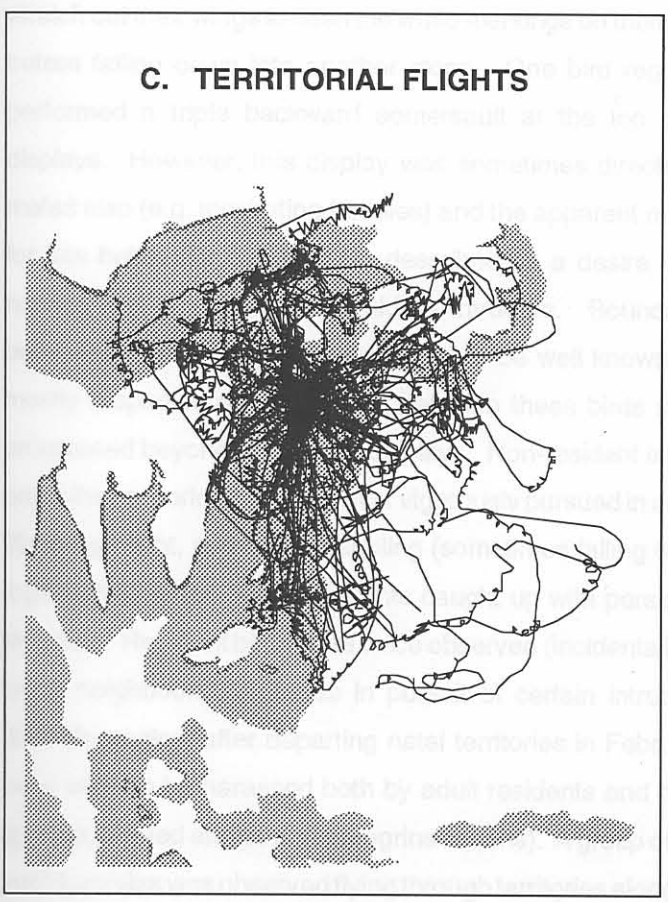
The average range of the four pairs indicated by these flight paths was 26,0 $km^2$, and it is clear from Figure 48 that overlap in the ranges was minimal. Boundaries between pairs often ran along distinct topographical features such as the long finger-like projection of middle plateau between KK and BR (Fig. 48 b & c). But boundaries were less well defined farther from nest sites (e.g. the southernmost koppie, known as the Pointer, shared by KK and BR). The flight paths indicated that PB shared 3,2% of their range with KK, but this represented 15,4% of KK's range; KK shared 6,9% of their range with BR, and 6,6% vice versa; BR shared 0,7% of their range with LH, and 0,3% vice versa. The average degree of overlap between neighbouring pairs was 5,5%. However it is likely that the full ranges of LH, BR and KK are underestimated because of limited observation time and difficulty in tracking these pairs. Incidental

University of Pretoria etd – Davies, R A G (1994)



observations indicated that the kloof between LH and BR (Gymnogene Gorge) was shared by both pairs, and that KK ranged farther east along the Pointer. So average range size for lower escarpment pairs may be larger than indicated by these flight paths and the degree of overlap between neighbours might approach 10%. Overlap between full ranges of neighbouring pairs does not necessarily confer overlap in foraging ranges. Intensive observations of the Penberi pair indicated that flights where hunting was the prime motive (mean flight distance 5,7km) were more confined to a core area than the far-ranging flights (mean flight distance 8,2km) where territorial display was the prime motive (Figure 50). Simple directional flight (perch to perch) was the third apparent major motive for flights, and these flights were short (mean flight distance 2,3km). Statistical comparison of complete flights (perch to perch) revealed that there was a highly significant difference in flight distance for these three major motives ($K^2$=69,7; d.o.f.=2; p<0,001).



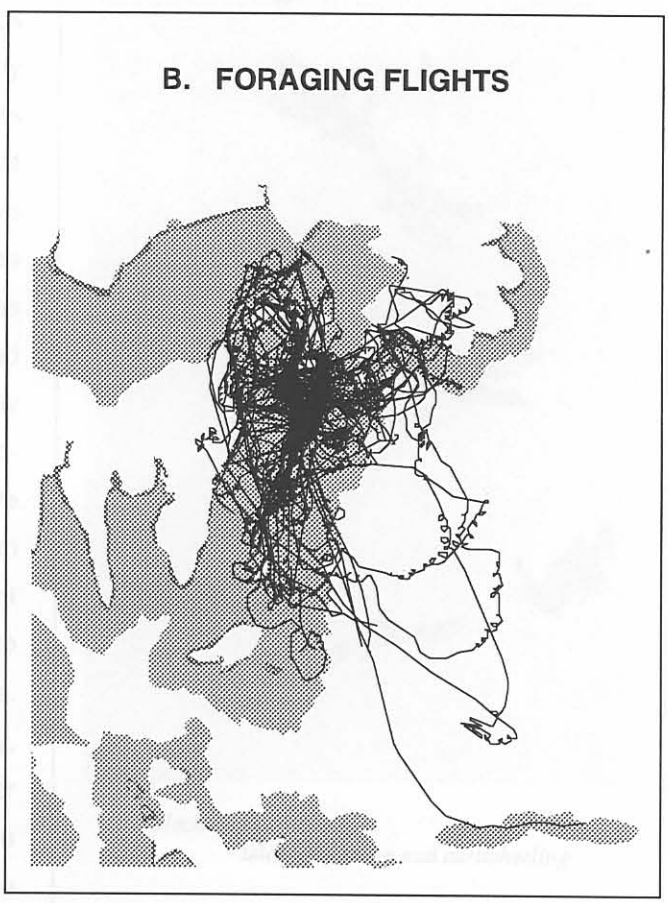




**Figure 50.** All flight paths of the Penberi eagles when their primary motive could be identified as (A) directional flight, (B) foraging behaviour, and (C) territorial behaviour. Some resolution was lost converting the ARCINFO coverages into WINDOWS METAFILE format, so the circling routes appear very angular. Elongated zig-zag routes are evident and these mark the location of pendulum displays (see text). Mountain slopes shaded.

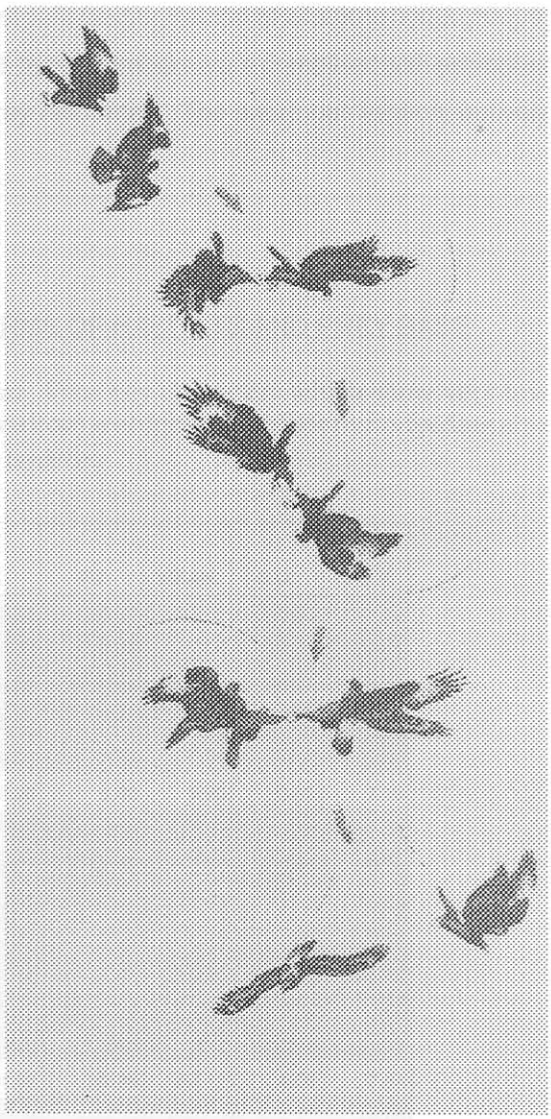
University of Pretoria etd – Davies, R A G (1994)



Territoriality appeared to be a very important component of black eagle behaviour and eagles allocated slightly more (7%) flying time to territorial display than to hunting. Incidental observations of upper escarpment pairs suggested that these birds invest more time in territorial behaviour and less time in foraging behaviour than lower escarpment pairs. Upper escarpment pairs have commanding views over lower escarpment territories and on one occasion an upper escarpment eagle (possibly LC) was observed to 'poach' a hyrax from a lower escarpment territory (BR) unnoticed by the territory holders. In interactions between upper escarpment and lower escarpment pairs, the upper escarpment birds usually appeared to be more dominant (chasing rather than fleeing).

*Territorial behaviour*

There were certain times, perhaps when flying conditions were best, when it appeared that all neighbouring pairs would suddenly ascend and soar over territorial boundaries at high altitude to interact with one another. Male eagles would often launch major territorial flights immediately after a kill, but most territorial flights were conducted in tandem. Territorial displays usually involved undulation or pendulum flights (Gargett 1990), where the birds would stall at the top of their momentum and stretch out their wings to flash the white markings on their back before falling down into another stoop. One bird regularly performed a triple backward somersault at the top of its displays. However, this display was sometimes directed at mates also (e.g. incubating females) and the apparent motive for this behaviour can best be described as a desire to be noticed and a warning to would-be intruders. Boundaries between neighbouring pairs appeared to be well known and mostly respected so aggression between these birds rarely progressed beyond undulation displays. Non-resident intruders to the territories were however vigorously pursued in active (flapping) flight, and talon-grappling (sometimes falling 600m together) occurred when residents caught up with persistent intruders. Resident birds were twice observed (incidentally) to cross neighbours' territories in pursuit of certain intruders. Juvenile eagles, after departing natal territories in February, were seen to be harassed both by adult residents and other species (booted eagles and peregrine falcons). A group of five such juveniles was observed flying through territories along the upper escarpment. Both escarpments appeared to be used as major 'flyways' by the non-breeding population. Harassment of a free-living, hand-raised eagle by wild resident adults in the KRNP became more intense when the hand-raised bird moulted into adult plumage.



*Black eagle aggression*
*- talon grappling and cartwheeling*

University of Pretoria etd – Davies, R A G (1994)



*A comparison of territories*

Some territories (e.g. PB) were much larger than others (e.g. KK). To elucidate whether this variation was due to behaviour of the owners or the distribution of resources, various characteristics were statistically compared (Table 14) for the four neighbouring territories where the prey base and its refuge environment had been intensively mapped by GIS (Chapters 3 & 4). Each slope in the mapped area (Chapter 3, page 29) was allocated to a particular territory on the basis of flight paths (earlier) and incidental observations of the pairs. Slope data were then summed according to territory. Slopes had been defined as they would be observed by foraging eagles, and as most territorial boundaries followed obvious topographical features such as ridges separating slopes, this approach seemed appropriate.

There was great variation in the extent of some of the major habitats and in the extent of areal rocky habitats defended by the pairs. Despite wide variation in territory size, all pairs defended remarkably similar amounts of mountain slopes, lineal rock outcrops, hyrax groups and especially the amount of safe feeding habitat available to hyrax groups. Variation between territories was not reduced when estimates of rock hyrax numbers were combined with estimates of red rock rabbit numbers to give a more complete overview of prey resources. The enormous territory actively

---

TABLE 14

A COMPARISON OF FOUR EAGLE TERRITORIES IN TERMS OF HABITATS AND PREY BASE

Surface area calculations included compensation for slope gradient. Four key characters which show very low variability (as expressed by standard deviation and coefficient of variation) are highlighted. Safe hyrax feeding area was calculated on the GIS as all areas within 15m of rocks in each territory.

| parameter | units | LH | BR | KK | PB | MEAN | S.D. | % C.V. |
|---|---|---|---|---|---|---|---|---|
| SURFACE AREA | km2 | 32.00 | 19.30 | 21.10 | 30.30 | 25.68 | 6.40 | 24.94 |
| BOTTOM PLAINS | km2 | 19.89 | 2.61 | 6.76 | 19.04 | 12.08 | 8.71 | 72.11 |
| LOWER SLOPES | km2 | 8.59 | 8.00 | 9.18 | 7.65 | 8.36 | 0.67 | 8.06 |
| MIDDLE PLATEAU | km2 | 3.59 | 8.72 | 5.17 | 1.79 | 4.82 | 2.95 | 61.14 |
| UPPER SLOPES | km2 | 0.00 | 0.00 | 0.00 | 1.79 | 0.45 | 0.90 | 200.00 |
| MOUNTAIN SLOPES | km2 | 8.60 | 8.00 | 9.20 | 9.40 | 8.80 | 0.63 | 7.19 |
| NUMBER OF OUTCROPS | # | 755 | 707 | 498 | 658 | 655 | 112 | 17.05 |
| ESCARPMENT | km | 10.38 | 16.07 | 11.01 | 12.32 | 12.45 | 2.55 | 20.48 |
| SANDSTONE + DYKES | km | 49.84 | 36.21 | 40.61 | 40.04 | 41.68 | 5.78 | 13.88 |
| KOPPIES + KNOLLS | km2 | 0.79 | 2.4 | 2.31 | 0.39 | 1.47 | 1.03 | 70.13 |
| SCREES | km2 | 1.77 | 2.33 | 2.75 | 2.97 | 2.46 | 0.53 | 21.52 |
| LARGE ROCKS | # | 14801 | 18854 | 23966 | 25626 | 20812 | 4936 | 23.72 |
| BOULDERS | # | 441 | 559 | 780 | 908 | 672 | 211 | 31.39 |
| TOTAL LINEAL OUTCROPS | km | 60.22 | 52.28 | 51.62 | 52.36 | 54.12 | 4.08 | 7.54 |
| TOTAL AREAL OUTCROPS | km2 | 2.56 | 4.73 | 5.06 | 3.36 | 3.93 | 1.17 | 29.83 |
| ROCK SURFACE AREA | km2 | 3.40 | 5.72 | 5.92 | 4.20 | 4.81 | 1.21 | 25.24 |
| SAFE HYRAX FEEDING AREA | km2 | 5.06 | 5.53 | 5.59 | 5.34 | 5.38 | 0.24 | 4.44 |
| CREVICES | # | 35464 | 48272 | 48688 | 44975 | 44350 | 6152 | 13.87 |
| HYRAX GROUPS | # | 67 | 66 | 59 | 59 | 63 | 4 | 6.93 |
| HYRAX | # | 1099 | 1082 | 968 | 968 | 1029 | 71 | 6.93 |
| RED ROCK RABBITS | # | 459 | 463 | 327 | 276 | 381 | 94 | 24.77 |
| PREY | # | 1558 | 1545 | 1295 | 1244 | 1410 | 165 | 11.66 |

University of Pretoria etd – Davies, R A G (1994)



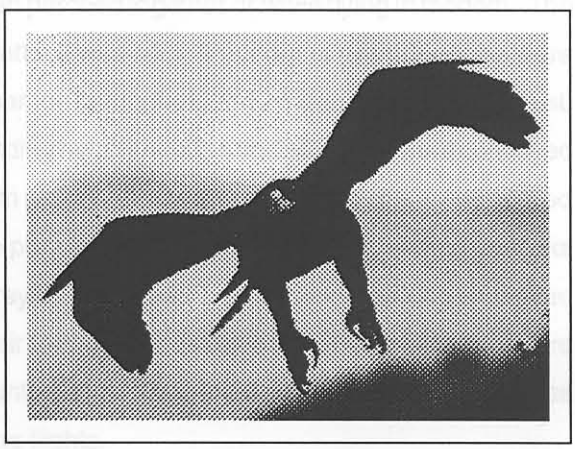
patrolled by the Penberi pair actually contained fewer estimated prey resources than the smaller neighbouring territories. It is not obvious from this analysis whether the eagles are able to defend their territories on the basis of hyrax numbers or on the basis of some closely-correlating variable such as mountain slopes or rocky habitat, which might be more easily assessed by the occupants. But it was particularly striking that three territories (BR, KK & PB) should each defend 52km of lineal rock outcrop (coefficient of variation <1% for this variable if LH is excluded), and that the safe feeding area available to hyrax showed the least variability of all parameters, between territories. Defence of greater amounts of lineal rock outcrops (60km) by LH may be compensatory for a lack of other hyrax refuge habitat in this territory, particularly screes.

*Strikes at prey*

Success of various black eagle foraging tactics could be appraised by considering the outcomes of strikes at prey. Strikes were defined as a definite and purposeful approach towards sighted prey. One strike was witnessed for every 2,6h continuous observations of eagles. One kill was witnessed for every 23,6h continuous observations of eagles. A total of 112 strikes at prey (mostly hyrax) were witnessed in the course of observations and other fieldwork, but only 106 provided complete data for interpreting success. Strikes were launched at distances ranging from 20 - 1900m (mean=679; s.d.=454). These distance measurements include no compensation for gradient of approach. On one occasion the Penberi pair spotted a karoo korhaan in the veld on the bottom plains at exactly 1965m distance and killed it after a flight lasting 1 min 32 sec (their flight speed in a fast glide was 77kph). There was no significant difference in the length of strikes made from perches and those made from searching flight. Most strikes were not far from nests (mean distance from nest=1143m; s.d.=707; range=220 - 3200). Of all strikes yielding complete data (n=106), nine resulted in kills. This represents a success rate of 8,5%. However many of the strikes were abandoned well before the eagles reached their prey. If these are excluded, the eagles achieved a success rate of 12,5%.

*Surprise attacks*

Only 9% of strikes were made at non-targeted hyrax which were encountered 'by surprise' as the eagles flew around rock outcrops, and none of these were successful. Eagles preferred to sight their prey first from a perch or from a high altitude flight (up to 600m above ground) and then make an attack, i.e. hunting by observation rather than expectation. Often the birds would fly off out of sight before making a concealed approach at high speed, low altitude and close together. Approach paths to prey were often (53% of strikes) estimated to be less than six metres above the ground. Cover was used on 42% of strikes, and the eagles attacked with the sun directly behind them on 12% of occasions. On a few occasions an attacking eagle was observed to take a very indirect route in order to position itself below the skyline against a low sun on its approach to prey.



University of Pretoria etd – Davies, R A G (1994)



*'Still hunting' versus 'active hunting'*

Eagles spent more time hunting from perches ('still hunting') than from searching flight ('active hunting'), but searching flight provided a higher prey encounter rate (0,79 strikes per hour) than perch hunting (0,26 strikes per hour), with the overall result that approximately equal numbers of strikes were made from both methods. The success rates of strikes launched from perches versus searching flight are summarised in Table 15. Strikes made while still hunting were approximately twice as successful as strikes made while active hunting, but these differences could not be demonstrated statistically.

TABLE 15

SUCCESS OF BLACK EAGLE STRIKES AT PREY:
STILL HUNTING VS. ACTIVE HUNTING, AND SOLO HUNTS VS. TANDEM HUNTS
(abandoned strikes included)

| | SOLO | TANDEM | SOLO + TANDEM |
|---|---|---|---|
| STILL HUNTING | 2/26 = 7,6% | 4/26 = 15,4% | 6/52 = 11,7% |
| ACTIVE HUNTING | 1/26 = 3,8% | 2/28 = 7,1% | 3/54 = 5,6% |
| STILL + ACTIVE | 3/52 = 5,8% | 6/54 = 11,1% | 9/106 = 8,5% |

*Co-operative hunting behaviour*

The success of strikes made while hunting in tandem or solo is also contrasted in Table 15. Tandem strikes were approximately twice as successful as solo strikes, but again this difference was not statistically significant. No successful solo strikes were observed until the Penberi pair were observed for five days during the incubation period in July 1989. Black eagle pairs monitored one another closely when perched together or while flying in tandem. The average estimated distance between mates during a high speed attack was 44m. Four out of five prey items were shared. Some smaller prey (a suricate and a karoo korhaan) and carrion (springbok) were eaten away from the nest. The suricate was killed outside the nesting period. Other prey, including hyrax juveniles and all adults, were conveyed to the nest cliff. Division of labour was apparent on 45% of tandem strikes and on four out of five closely witnessed kills by pairs. During an attack the female would usually flush the prey from cover (sometimes by landing on rocks or bushes), while the male would hang overhead and catch the prey as it flushed. This method was also employed by a resident pair of eagles attacking an intruding sub-adult in their territory. Females were observed to flap more to keep up with males in light airs. Males initiated most of the hunting flights and led 82% of the observed strikes at prey. Females were more inclined to terminate tandem hunting flights.

University of Pretoria etd – Davies, R A G (1994)



*Movements of male, female and juvenile black eagles within their territory*

Intensive observation of the Penberi pair provided sufficient data to compare movements of the pair together, the male alone, the female alone and the 1989 fledgling (Figure 51). Most flights, particularly the far-ranging territorial flights were conducted as a pair. Extensive solo flying by the male was mainly recorded during the incubation period and it is apparent that the male preferred to remain in the core foraging area near to the nest. Female solo movements were very limited and mainly restricted to the nest area. Flights by the pair were longer (mean distance 6,1km; s.d. 6,5) than flights by the male (mean distance 4,1km; s.d. 4,3) or flights by the female (mean distance 2,2km; s.d. 2,1). These differences were statistically highly significant ($K^2$=12,5; d.o.f.=2; p<0,01). Flights of the juvenile (for 5d about 2,5mth after fledging) were also very limited and restricted to a kloof behind the nest area. The juvenile did not accompany the adults on long flights and was not involved in any of their hunting behaviour.

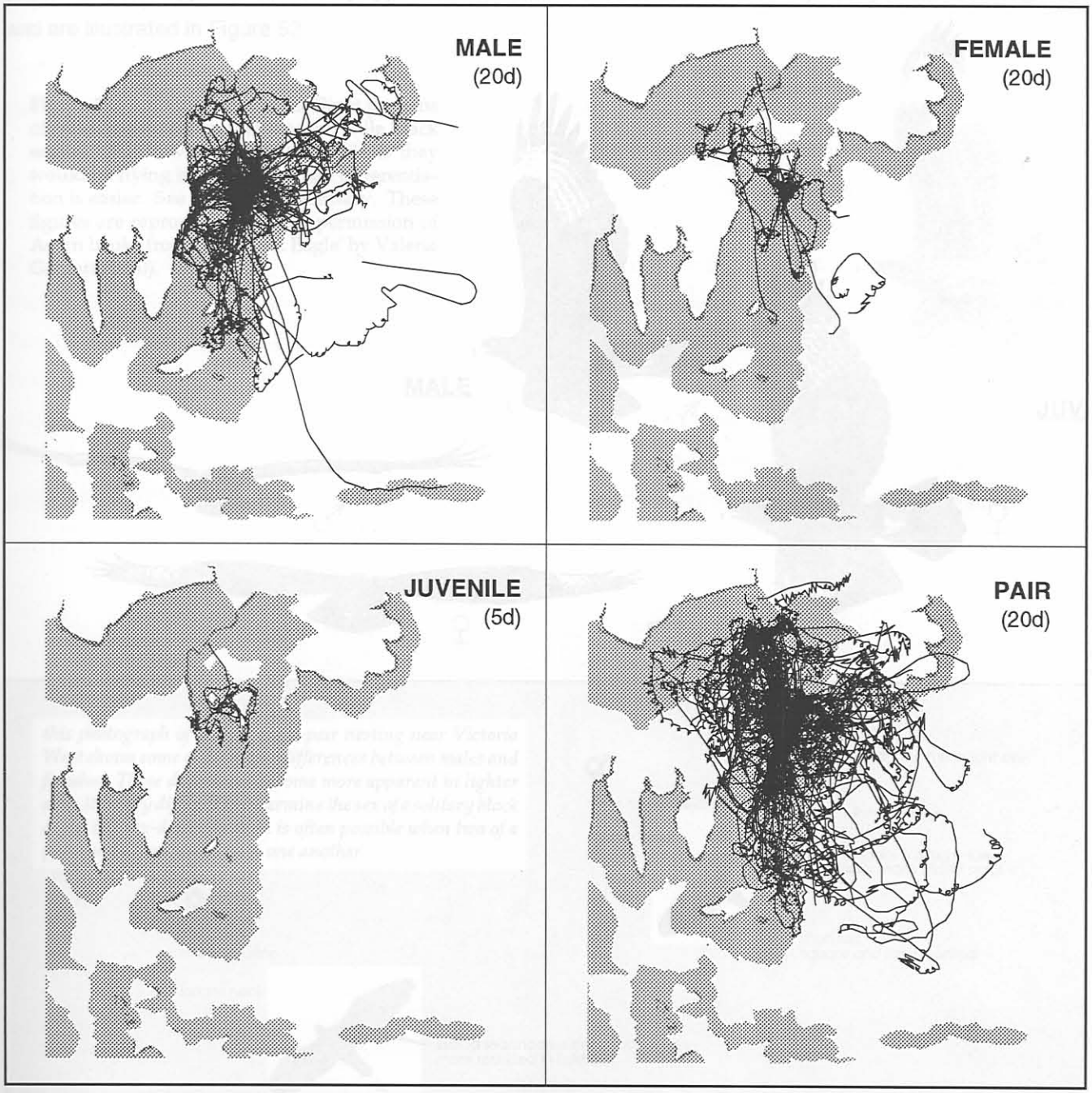



**Figure 51.** All flight paths of the Penberi eagles separated for tandem flights, solo flights by the male, solo flights by the female, and solo flights by the juvenile. Observation periods are given in brackets. Mountain slopes in grey, escarpment in dark grey.

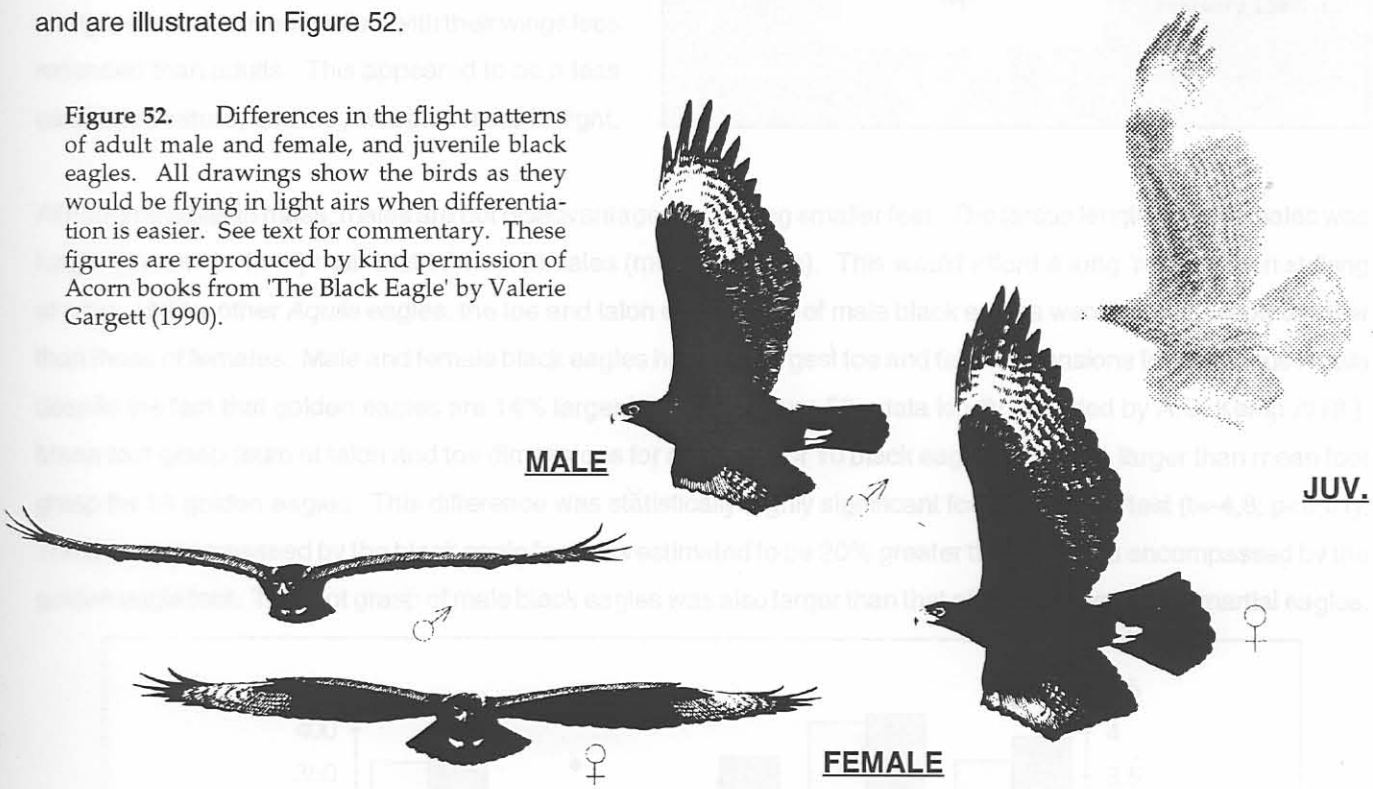
University of Pretoria etd – Davies, R A G (1994)

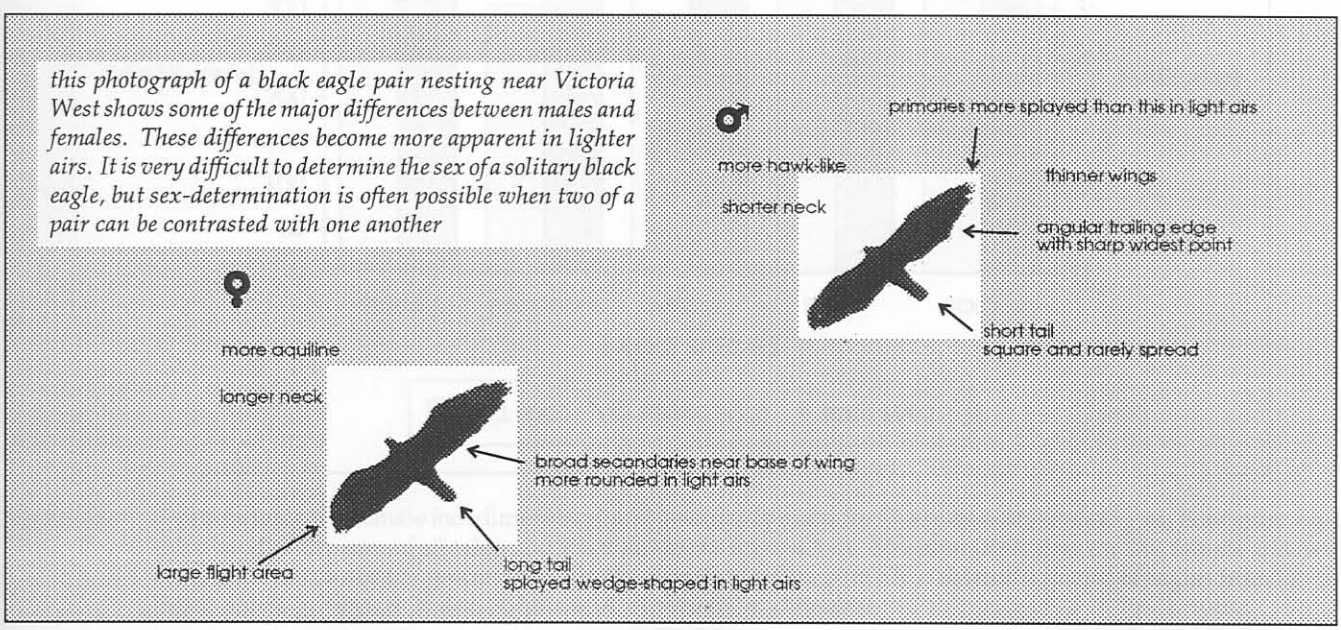


*Morphometrics of male, female and juvenile black eagles*

Body dimension data were available for 16 individual black eagles (pers. rec.; A.C. Kemp *in litt.*). Females weighed 13% more than males. Females differed in shape from males: wing areas were 9% larger and tail area was 53% larger (total flight surfaces of females were 15% larger than those of males). Unlike males, females often flew with their large, wedge-shaped tails expanded (Gargett 1990; pers. obs.). Female wings are broader and more rounded at the secondaries, and females fly with their wings more flexed at the carpal joint - consequently the 'finger-tips' of their outer primary feathers are usually less emarginated. Male wings are thinner and more angular with a sharp widest point visible in the trailing edge of the secondaries - this widest point often looks farther out from the torso than on females, but this could be because males usually hold their wings fully outstretched in a slightly negative dihedral posture which is apparent when they approach head-on. These differences were especially noticeable in light airs and are illustrated in Figure 52.

**Figure 52.** Differences in the flight patterns of adult male and female, and juvenile black eagles. All drawings show the birds as they would be flying in light airs when differentiation is easier. See text for commentary. These figures are reproduced by kind permission of Acorn books from 'The Black Eagle' by Valerie Gargett (1990).

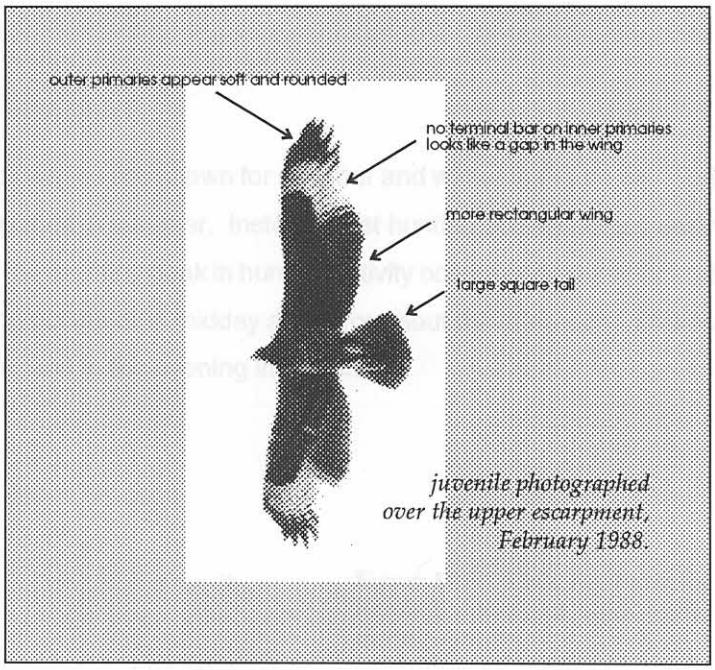


University of Pretoria etd – Davies, R A G (1994)



Differences were also apparent between dimensions of the flight surfaces of juvenile and adult black eagles (see Fig. 52 and accompanying photograph). Juveniles have a large square tail and lack the characteristic bulging secondary feathers of adults. Second plumage secondaries of a hand-raised female eagle were 20 mm longer than the juvenile feathers. The centre (deck) tail feather of this bird became 5 mm shorter in second plumage, and the outer tail feathers became 12 mm shorter, i.e. the tail of this female became smaller and more wedge-shaped. Juveniles flew with their wings less extended than adults. This appeared to be a less confident posture, and they wobbled more in flight.




Although smaller in mass, males are not disadvantaged by having smaller feet. The tarsus length of most males was longer (mean=114mm) than that of most females (mean=111mm). This would afford a long 'reach' when striking at prey. Unlike other *Aquila* eagles, the toe and talon dimensions of male black eagles were not noticeably smaller than those of females. Male and female black eagles have the largest toe and talon dimensions for the genus *Aquila* despite the fact that golden eagles are 14% larger by mass (Figure 53 - data kindly provided by A.C. Kemp *in litt.*). Mean foot grasp (sum of talon and toe dimensions for one foot) for 10 black eagles was 10% larger than mean foot grasp for 10 golden eagles. This difference was statistically highly significant for a two-tailed test ($t=-4,8$; $p<0,01$). The area encompassed by the black eagle foot was estimated to be 20% greater than the area encompassed by the golden eagle foot. The foot grasp of male black eagles was also larger than that of male crowned and martial eagles.

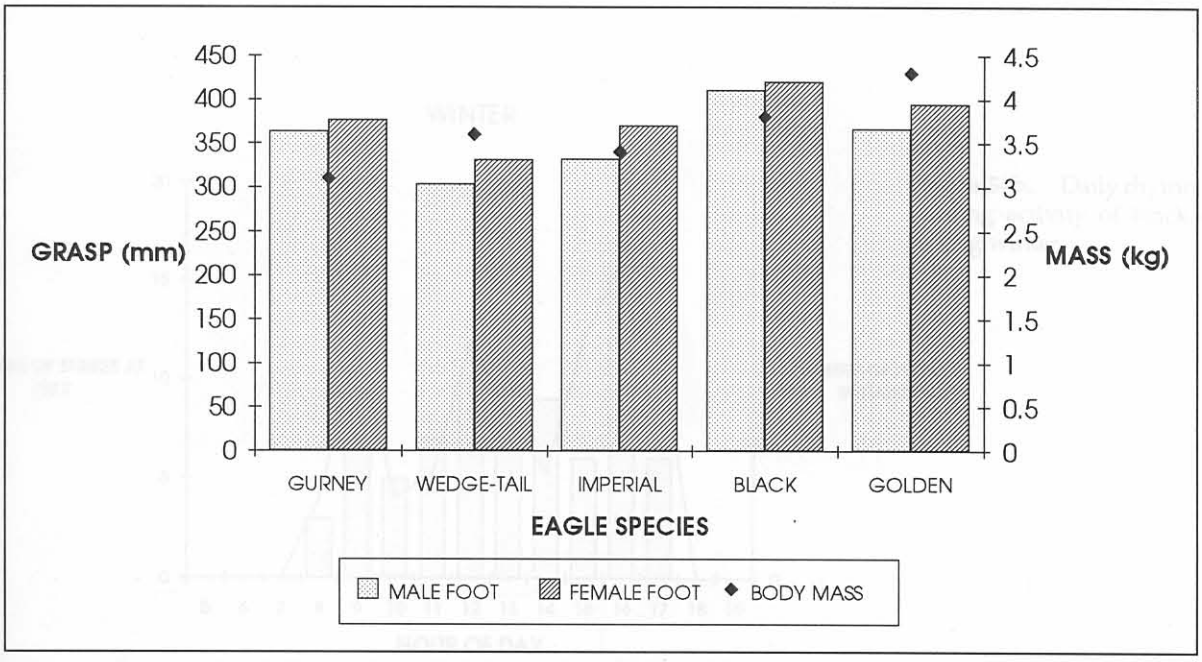



**Figure 53.** Average male and female foot dimensions, and mean body mass, for five species of *Aquila* eagles. Foot grasp was calculated as the sum of all talon and toe dimensions for one foot. Morphometric data for five female and five male individuals of each species were kindly supplied by Kemp (*in litt.*). Scientific names of eagles from left to right: *Aquila gurneyi, A. audax, A. heliaca, A. verreauxii, A. chrysaetos.*

University of Pretoria etd – Davies, R A G (1994)



*The influence of season on black eagle behaviour*

Daily activity rhythms in the hunting behaviour of black eagles are shown for summer and winter in Figure 54. The midday peak in activity is an hour earlier and less apparent in summer. Instead most hunting activity occurs early morning (08h00) and late evening (18h00). In winter, the morning peak in hunting activity occurs one hour later and the evening peak two hours earlier. Extensive hunting occurs over midday and throughout the afternoon. Strikes at prey were more frequent in the morning in summer, and in the evening in winter.

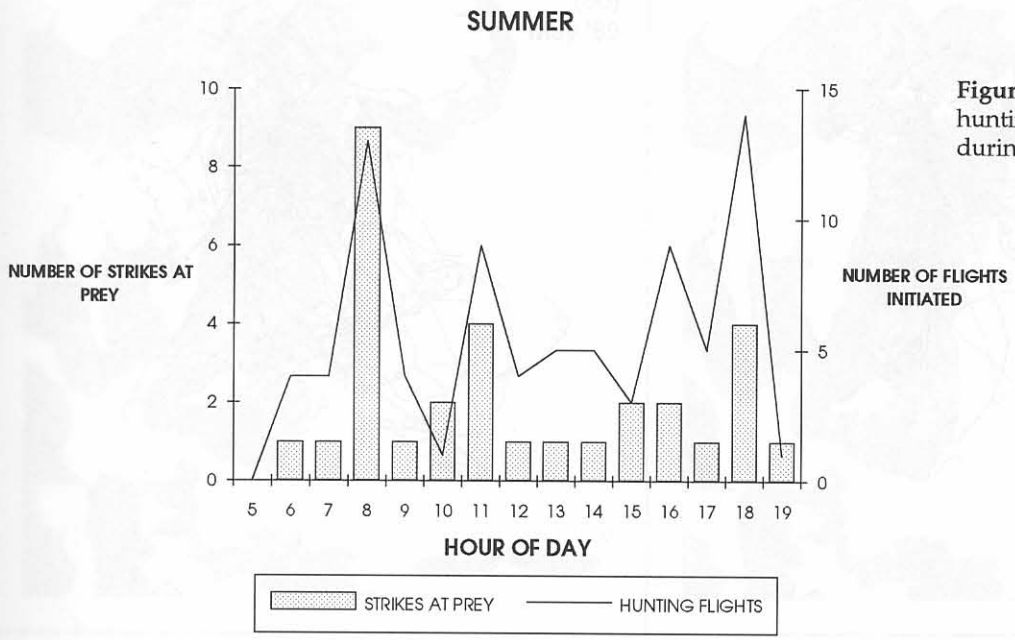



**Figure 54a.** Daily rhythm in the hunting activity of black eagles during summer.

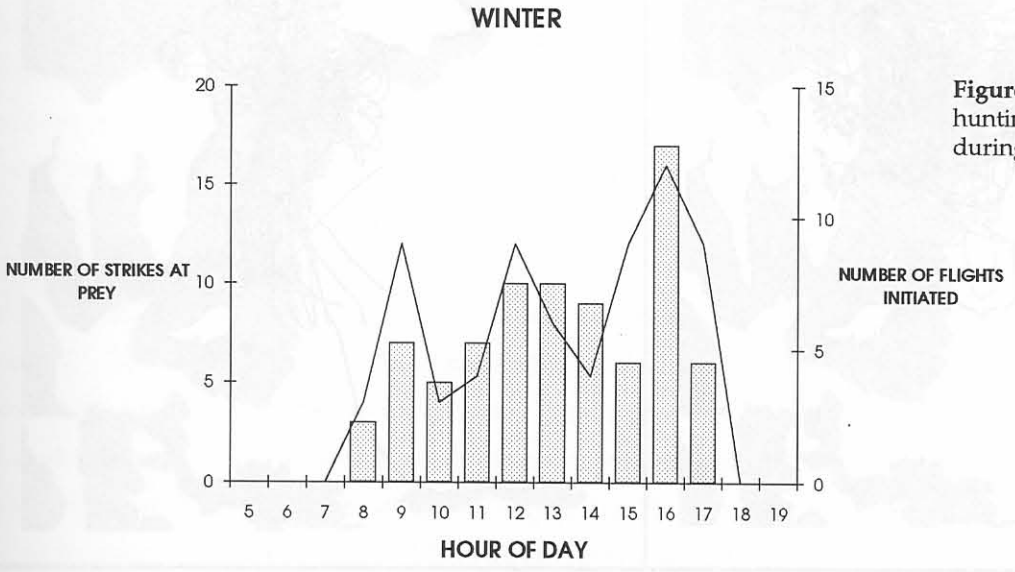



**Figure 54b.** Daily rhythm in the hunting activity of black eagles during winter.

University of Pretoria etd – Davies, R A G (1994)



Movements of the Penberi pair during the four major periods in the year (pre-breeding, incubation, nestling, fledgling) are shown in Figure 55. Movements were far-ranging and less nest-site bound during the pre-breeding and fledgling periods. Territorial displays were most frequent during the fledgling period and least frequent prior to breeding. The pair spent more time together, and more time perching prior to breeding. Movements were very concentrated around the nest site while there were eggs or small chicks in the nest. During the fledgling period, the pair were far-ranging but centred their activity around the area slightly above the nest site where the fledgling was resident, and did not venture far away over the plains. There was no significant difference in the length of flights for different seasons.

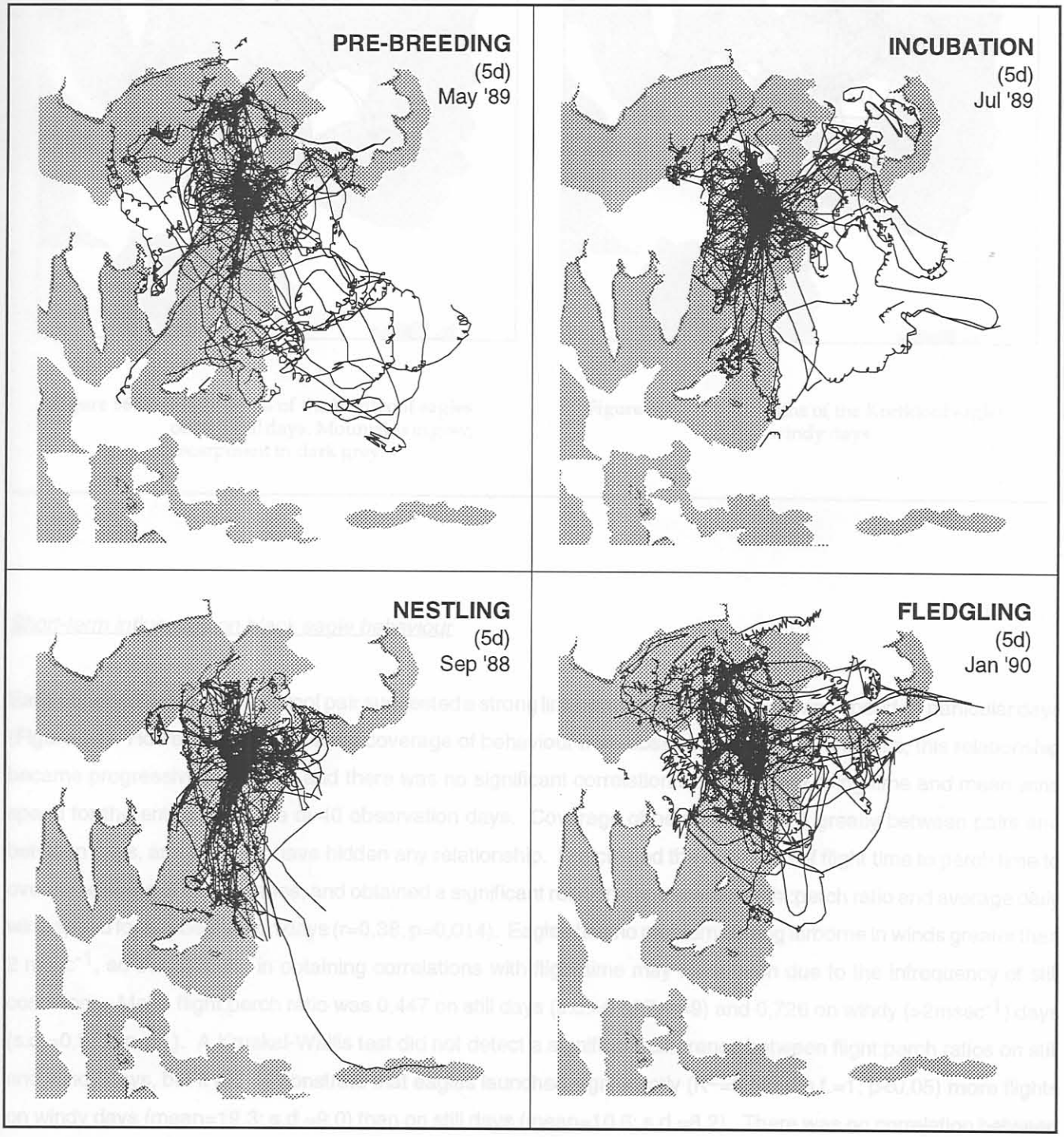



**Figure 55.** All flight paths of the Penberi eagles separated for the four major periods in a black eagle's year: pre-breed ing (112-142d), incubation (45d), nestling (88d) and post-fledging (90-120d). Duration and timing of observa tion periods are supplied. Mountain slopes in grey, escarpment in dark grey.

University of Pretoria etd – Davies, R A G (1994)



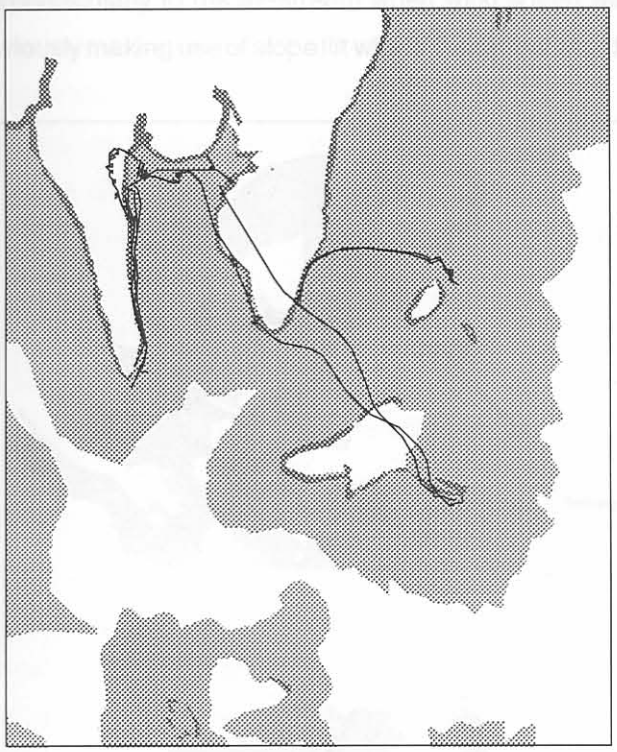


**Figure 56a.** Flight paths of the Kortkloof eagles on two still days. Mountains in grey, escarpment in dark grey.

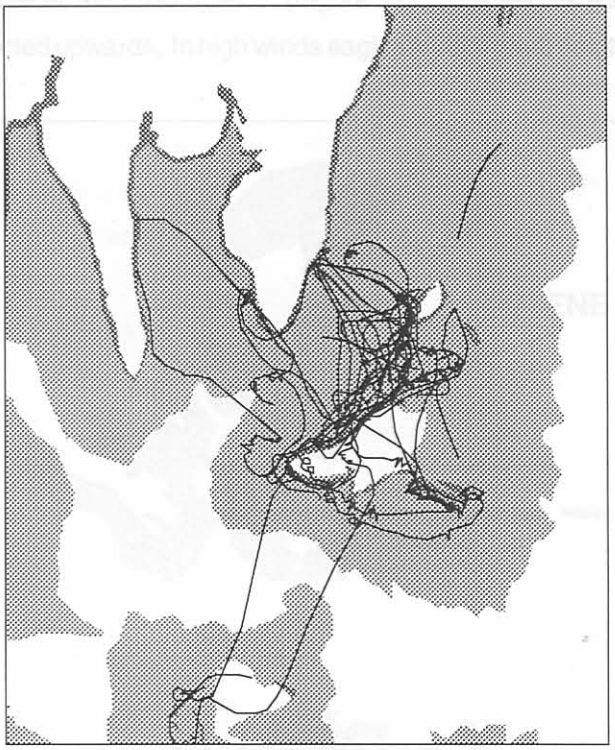


**Figure 56b.** Flight paths of the Kortkloof eagles on two windy days

*Short-term influences on black eagle behaviour*

Early observations of the Kortkloof pair suggested a strong link between flying time and wind speed on particular days (Figure 56). However, with increased coverage of behaviour from observations of different pairs, this relationship became progressively obscure and there was no significant correlation between daily flying time and mean wind speed for the entire database of 40 observation days. Coverage of behaviour varied greatly between pairs and between days, and this may have hidden any relationship. I calculated the daily ratio of flight time to perch time to overcome some of these biases, and obtained a significant relationship between flight:perch ratio and average daily wind speed for all observation days (r=0,38; p=0,014). Eagles had no problem getting airborne in winds greater than 2 $msec^{-1}$, so the difficulty in obtaining correlations with flight time may have been due to the infrequency of still conditions. Mean flight:perch ratio was 0,447 on still days (s.d.=0,527; n=9) and 0,726 on windy (>2$msec^{-1}$) days (s.d.=0,972; n=31). A Kruskal-Wallis test did not detect a significant difference between flight:perch ratios on still and windy days, but it did demonstrate that eagles launched significantly ($K^2$=5,52; d.o.f.=1; p<0,05) **more** flights on windy days (mean=19,3; s.d.=9,0) than on still days (mean=10,6; s.d.=8,2). There was no correlation between the distance or duration or speed of flights and wind speed recorded actually during those flights.

University of Pretoria etd – Davies, R A G (1994)



Wind direction had a more obvious influence on black eagle flying. Eagles clearly favoured slopes orientated perpendicularly to the air-stream when wind speed was greater than two msec$^{-1}$ (Figure 57). The eagles were obviously making use of slope lift where the airflow was deflected upwards. In high winds eagles rose to great heights

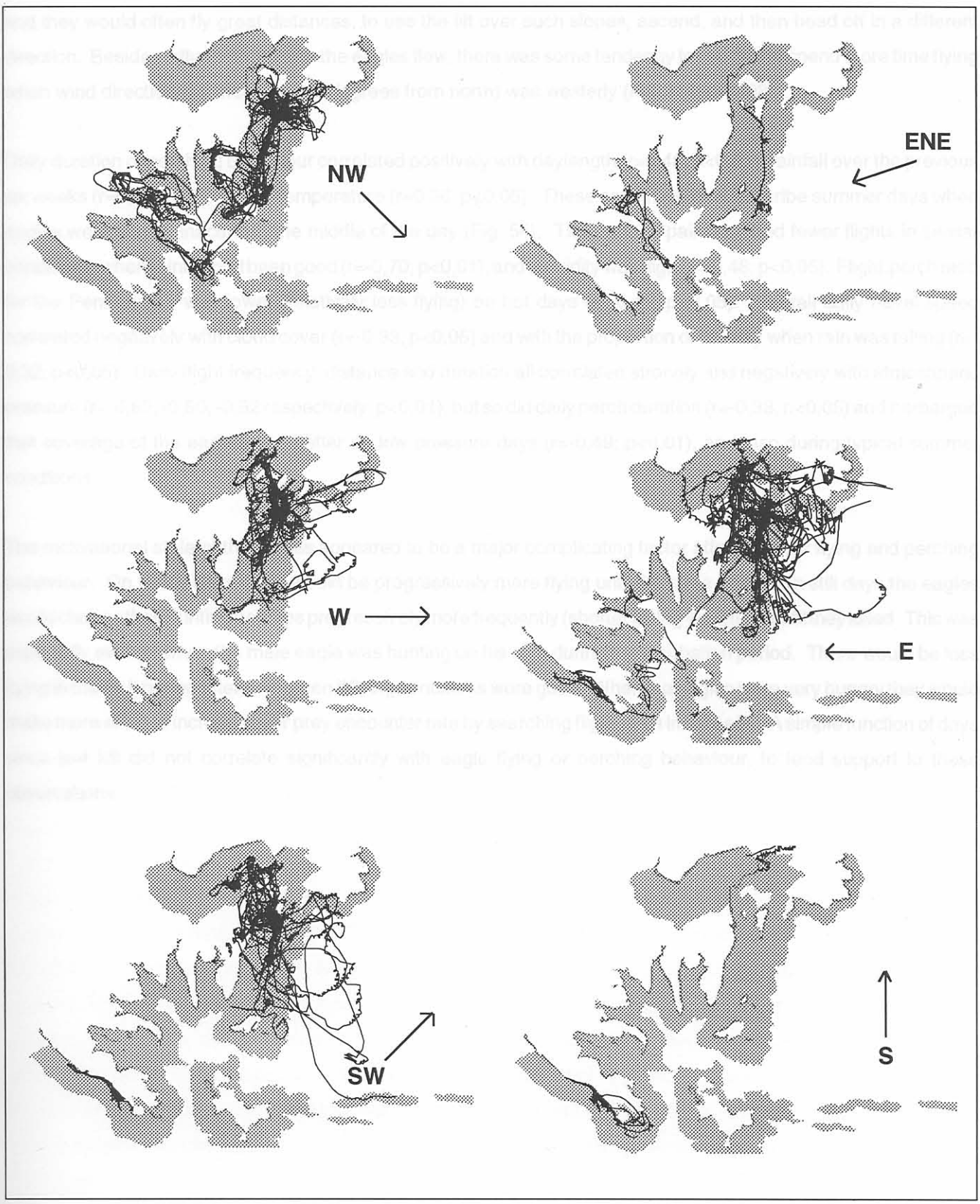



**Figure 57.** Flight paths for all eagle pairs for different wind directions, when wind was greater than 2msec$^{-1}$. Mountains in grey, escarpment in dark grey. Consult TIN-model on page 17 for 3-D topography.

University of Pretoria etd – Davies, R A G (1994)



above and beyond such slopes, apparently using 'wave' airflow. Black eagles can fly in the strongest of gales. On one occasion wind speed over the Penberi ridge was recorded at 157kph and the eagle pair were hanging motionless overhead, with a slight adjustment of wingshape the eagles moved steadily headlong into the gale without any obvious loss of height. Bowls or amphitheatres facing the airflow were particularly favoured by slope-soaring eagles, and they would often fly great distances, to use the lift over such slopes, ascend, and then head off in a different direction. Besides influencing where the eagles flew, there was some tendency for eagles to spend more time flying when wind direction (as measured in degrees from north) was westerly ($r=0,314$; $p=0,08$).

Daily duration of perching behaviour correlated positively with daylength ($r=0,48$; $p<0,01$), rainfall over the previous six weeks ($r=0,61$; $p<0,01$), and temperature ($r=0,36$; $p<0,05$). These conditions best describe summer days when eagles were largely inactive in the middle of the day (Fig. 54). The Penberi pair launched fewer flights in similar conditions: when rainfall had been good ($r=-0,70$; $p<0,01$), and humidity was high ($r=-0,48$; $p<0,05$). Flight:perch ratio for the Penberi pair was lower (relatively less flying) on hot days ($r=-0,45$; $p<0,05$). Overall daily travel speed correlated negatively with cloud cover ($r=-0,33$; $p<0,05$) and with the proportion of the day when rain was falling ($r=-0,32$; $p<0,05$). Daily flight frequency, distance and duration all correlated strongly and negatively with atmospheric pressure ($r=-0,62$, $-0,50$, $-0,52$ respectively; $p<0,01$), but so did daily perch duration ($r=-0,38$; $p<0,05$) and it emerged that coverage of the eagles was better on low pressure days ($r=-0,49$; $p<0,01$), and also during typical summer conditions.

The motivational state of the eagles appeared to be a major complicating factor affecting their flying and perching behaviour. On windy days there would be progressively more flying until the birds killed. On still days the eagles would change their hunting perches progressively more frequently (shorter giving-up times) until they killed. This was especially evident when the male eagle was hunting on his own during the incubation period. There would be less flying in the 24 h period after a kill, even if flying conditions were good. When the eagles were very hungry they would make more effort to increase their prey encounter rate by searching flight even in light airs. A simple function of days since last kill did not correlate significantly with eagle flying or perching behaviour, to lend support to these observations.

University of Pretoria etd – Davies, R A G (1994)



# DISCUSSION

## *Distribution and abundance*

Regular territorial spacing in raptors can usually be attributed to an even, predictable and defensible prey base, and has the effect of minimizing interference in the hunting and breeding behaviour of neighbouring conspecifics (Newton 1979). The G-value of 0,79 calculated from nearest neighbour distances between active nests of black eagles in the Nuweveld Mountains at Beaufort West suggests that this population is regularly spaced, and this corresponds to a relatively even distribution of hyrax groups within the rocky habitats that the eagles defend (Chapter 4).

Spacing patterns of golden eagle pairs are often more regular than this (G-values range between 0,84 and 0,94: Tjernberg 1985; Watson & Rothery 1986). The lower G-value obtained in the present study can mainly be attributed to the closer nest spacing between upper escarpment pairs than between lower escarpment pairs, but higher variability in black eagle nest spacing has also been ascribed to patchy distribution of nesting habitat within relatively small ranges (Gargett 1990), and the spacing of other *Aquila* eagles has been found to be more variable in arid regions (Murphy 1975; Beecham & Kochert 1975; Ridpath & Brooker 1987). Less regular spacing of black eagle nest sites may also be related to patchy distribution of the refuge microhabitats used by hyrax in some areas.

On the basis of a nearest neighbour analysis of nest spacing, black eagle pairs in the Nuweveld Mountains at Beaufort West approach the same proximity recorded for black eagle pairs in the Matobo Hills, Zimbabwe (Table 16). This similarity might be an artefact produced by differences in the two dispersion patterns for the estimates of density in the two study areas are markedly different (Table 16). The black eagle population in the Matobo Hills, with an overall average territory size of 10,5km$^2$, remains the highest nesting density recorded for a large eagle species anywhere in the world, excluding the piscivorous *Haliaeetus* spp. (Newton 1979; Gargett 1990). Unlike the Matobo population, the study population at Beaufort West can be considered as linearly distributed along two escarpments. Spacing of sequential pairs along these escarpments is compared with other similar populations distributed linearly along mountain ranges in Table 16. Black eagle pairs evidently nest closer together along the upper escarpment at Beaufort West than along any other escarpment or ridge investigated to date.

A wider spacing between black eagle pairs nesting at lower altitude has also been noted by Brown (1988) for the Drakensberg escarpment and foothills. The wider spacing of sequential pairs along the lower escarpment at Beaufort West was similar to that recorded by Boshoff & Palmer (1988) for a population about 80km west along the Nuweveld range at Fraserberg, but both these populations are still more closely spaced than any other populations along linear mountain features in southern Africa. Nest sites are unlikely to be limiting along such escarpments so one might surmise that closer nesting along the Karoo escarpments is permitted by a greater abundance of rocky habitats and associated hyrax populations. Each kilometre of upper escarpment was associated with 3,5 km of other linear rock outcrops (mainly sandstone lenses), 35 ha of screes and 7,1 hyrax groups on the upper slopes; each kilometre of lower escarpment was associated with 2km of linear outcrops, 12 ha of screes and 4,7 hyrax groups on the lower slopes (Chapters 3 & 4). By defending four times as much escarpment, lower escarpment pairs evidently enjoy greater quantities of rock outcrop and hyrax groups, but they must cope with less convenient flying conditions.

University of Pretoria etd – Davies, R A G (1994)



TABLE 16

NEST-SPACING AND DENSITY OF BLACK EAGLE PAIRS IN THIS AND OTHER STUDIES

consult Fig. 3 for locations of mountain ranges

| LOCATION | NO. PAIRS | MEAN (km) | Std. Dev. | Coeff. Var. (%) | RANGE | SOURCE |
|---|---|---|---|---|---|---|
| *nearest neighbours analysis of nest-spacing:* | | | | | | |
| Matobo Hills 1979 | 38 | 2,6 | | | | Gargett (1990) |
| Matobo Hills (park) | | 2,0 | | | | Gargett (1990) |
| Nuweveld, Beaufort West | 20 | 2,7 | 1,0 | 37 | 1,3 - 4,5 | present study |
| Nuweveld, Fraserberg | 13 | 3,5 | 0,6 | 17 | 2,8 - 4,7 | Boshoff & Palmer (1988) from figure |
| Drakensberg | 8 | 6,2 | 1,5 | 24 | 4,9 - 8,8 | Brown (1988) from figure |
| *sequential pairs analysis of nest-spacing:* | | | | | | |
| Magaliesberg | 13 | 9,5 | 4,5 | 47 | 3,0 - 19,5 | Tarboton & Allan (1984) |
| Waterberg, Transvaal | 11 | 13,3 | 6,5 | 49 | 5,0 - 12,0 | Tarboton & Allan (1984) |
| Soutpansberg | 8 | 6,8 | 4,0 | 59 | 2,0 - 14,5 | Tarboton & Allan (1984) |
| Drakensberg escarpment | 5 | 5,8 | | | 4,8 - 6,5 | Brown (1988) |
| Drakensberg foothills | 3 | 8,6 | | | 8,3 - 8,9 | Brown (1988) |
| Waterberg, Namibia | 7 | 9,8 | | | | Brown & Cooper (1987) |
| Nuweveld, Fraserberg | 13 | 4,3 | 1,4 | 33 | 3,0 - 7,5 | Boshoff & Palmer (1988) |
| Nuweveld, BW upper esc. | 8 | 2,7 | 1,0 | 37 | 1,5 - 4,3 | present study |
| Nuweveld, BW lower esc. | 11 | 4,6 | 1,5 | 33 | 3,0 - 7,1 | present study |
| *density analysis* | | | | | | |
| Matobo Hills (park) | 39 | varied from 8,8 - 11,3 km2/pair | | | | Gargett (1990) |
| Matobo Hills (communal) | 26 | 35,0 km2/pair | | | | Gargett (1990) |
| Nuweveld, Fraserberg | 13 | @15,0 km2/pair (probably 23,3) | | | | Boshoff & Palmer (1988) |
| Nuweveld, Beaufort West | 18 | 24,0 km2/pair | | | | present study |
| Magaliesberg | 13 | 35,0 km2/pair (probably larger) | | | | Allan (1988) |
| Drakensberg | 8 | 65,0 km2/pair | | | | Brown (1988) |
| Karoo | | 65,0 km2/pair | | | | Siegfried (1968) |
| Kenya | 1 | 65,0 km2/pair | | | | Rowe (1947) |

*Aquila* eagles can subsist at relatively high densities in unstable environments by relying on periodic abundances of food such as carrion (Watson & Langslow 1989) and rabbits (Ridpath & Brooker 1987); but both these studies revealed that breeding is always more successful in regions where a suitable and predictable prey base exists. The tall cliffs and huge boulders encompassed by the small territories of the upper escarpment pairs are probably havens

University of Pretoria etd – Davies, R A G (1994)



for hyrax when populations are not depressed by drought. But these territories offer little in terms of alternative prey when the hyrax population crashes as occurred in the KRNP between 1981 and 1984 (Chapters 1 & 4). Despite their appearance as optimal black eagle habitat - harbouring high densities of usually more dominant pairs, the upper escarpment territories can be considered inferior and less reliable in terms of the prey base, and this is borne out by the greater breeding effort and success of the lower escarpment pairs.

Black eagles are considered to be more territorial in the Matobo Hills where they occupy small defensible ranges (Gargett 1990), than in the Drakensberg where widely-spaced patches of rocky habitat lead to large areas of overlap and unused space between neighbouring pairs (Brown 1988). The present study indicated minimal overlap between pairs (5,5%), especially between their foraging ranges. There was very little evidence of unused space by the pairs. On this basis it seems fair to assume that the average territory size of 18 well-known pairs within the 435 $km^2$ study area would be 24,2 $km^2$. The indications of greater incidence of territorial intrusions on the upper escarpment may be associated with frequent use of the upper escarpment as a 'flyway' by non-breeding birds, and/or small prey populations in the upper escarpment territories.

Study pairs with access to plains within their territories often ranged several kilometres away from the mountainous areas. For this reason, the assumption that black eagles only occupy mountainous terrain probably led to significant under-estimation of territory size in the very similar Fraserberg terrain by Boshoff & Palmer (1988), and perhaps along the Magaliesberg range by Allan (1988), see Table 16. Territory sizes given for the Fraserberg pairs were probably further underestimated by the assumption of circular non-overlapping ranges. Neatly interlocking territories were observed in the present study and also in the Matobo (Gargett 1990).

The nesting distribution of the Fraserberg birds within the area searched (about 303$km^2$) actually suggests a density of 4,3 pairs/100$km^2$ and an average territory size of 23,3 $km^2$ (assuming interlocking territories with no overlap and no unused space). The similarity of this nesting density with that of the Beaufort West population (4,1 pairs/100$km^2$) suggests that estimation of the total population in the Nuweveld Mountain range (152 pairs) by extrapolation is valid.

Using the same density estimate to predict population sizes for the other stretches of continental escarpment in the Karoo may be criticized on the grounds that rainfall and productivity vary between these ranges. But topography of the Roggeveld range is highly similar, and the Sneeuberg and Winterberg ranges are about twice the width of the Nuweveld range so the total population estimate of 600 resident pairs along the Karoo escarpments is likely to be very conservative. These ranges represent just over one quarter of the mountainous regions in the Cape. Other Cape mountain ranges, the Cape fold mountains (comprising 68% of remaining mountain regions) and the Drakensberg (9% remainder), probably accommodate black eagles at lower density than the Karoo escarpments. Black eagles also occur on scattered isolated koppies throughout the Karoo which would not have been incorporated into the calculated area of the mountainous regions. So it seems likely that the black eagle population in the Cape Province greatly exceeds the estimate of 487 pairs (range 280-730) predicted from a questionnaire survey by Boshoff & Vernon (1980). If black eagles occur at the lowest recorded nesting density (60$km^2$/pair) in the remaining mountain ranges of the Cape Province (90305$km^2$), this would yield a minimum population estimate of nearly 2000 pairs in the Cape (excluding any pairs nesting outside major mountain ranges).

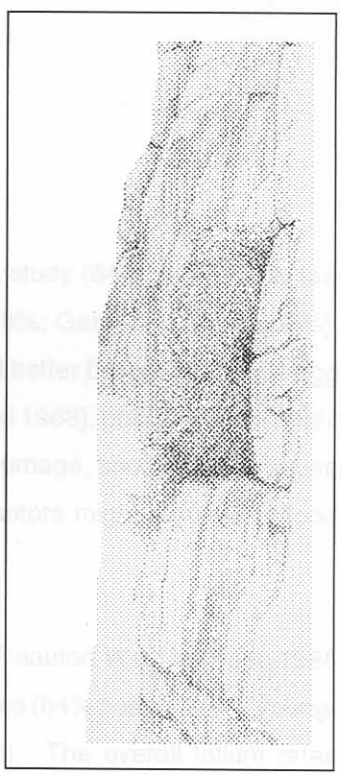
University of Pretoria etd – Davies, R A G (1994)



The increment to include the non-breeding population is probably also conservative because of a very probable bias towards territorial birds in the flight-frequency ratio. However it probably represents a minimum increment. Non-breeders would be much more abundant in mountainous areas lacking nest cliffs. Immatures often comprise about 30% of eagle populations (Brown & Watson 1964; Boeker & Ray 1972; Watson 1990). In the present study they comprised up to 40% of the non-breeding population. Following the incidents of adult mortality, mate-replacement took place in relatively short periods of time. This indicates a healthy floating population and adequate recruitment. Such is not the case for tawny and martial eagles on farmland in Namibia (Brown 1991). The healthy status of the black eagle population in the Cape can be ascribed to a few factors: black eagles rarely scavenge so they are less susceptible to strychnine poisoning (Allan 1989); they inhabit remote areas so direct persecution is difficult; and farmers in the Cape are changing their attitudes towards these birds thanks to major conservation efforts such as the postal survey conducted by Boshoff & Vernon (1980).

*Choice of nest-site*

Usually, an abundance of alternative nest sites is taken to indicate that a particular population is not limited by the availability of suitable sites. The correlation established in the present study and put forward by Gargett (1990), between abundant alternative sites and high failure rate indicates that this can be far from the case, and that failure stimulates 'frustration' nest-building at other sites.



Unlike other eagle populations where breeding failure usually occurred at the egg stage (Hustler & Howells 1986, 1987; Allan 1988; Gargett 1990), the Beaufort West black eagles were mainly failing at the small chick stage (55-64% all failures). Various lines of evidence suggest that much of this failure was caused by terrestrial predators. First, nests were preferentially located on tall cliffs no doubt since small cliffs experienced a higher failure rate (lower siting of nests on very tall cliffs may be to reduce risk of injury to fledging eagles). Secondly, the eagles avoided nesting on sandstone cliffs which also experienced higher failure rate. This substrate is richer in crevices (200ha$^{-1}$) than dolerite cliffs (78 crevices ha$^{-1}$) (Chapter 3), and thus can be considered more accessible to terrestrial predators. These factors would not influence accessibility to avian predators.

But most conclusively, the time-lapse cameras actually revealed predation by the small grey mongoose *Galerella pulverulenta* on black eagle nestlings, two years in a row at one very accessible site. It is anomalous to consider that a top predator such as the black eagle is at risk of predation to one of its prey species, but small grey mongooses are known to be very rapacious and have been observed to kill ostrich chicks (D. Conroy pers. comm.) and to challenge a female kori bustard on her nest (Allan 1987 unpubl., pers. comm.). Baboons are also considered to be a threat to nesting black eagles (Gargett 1990) and it may be relevant that the destruction or disintegration of two nests in the KRNP occurred on the more accessible sandstone cliffs which are favoured by baboons as roost sites.

University of Pretoria etd – Davies, R A G (1994)



Black eagles might be expected to be more prone to nest predation than other large eagles through low nest attendancy due to their preferential habit of tandem hunting, especially when prey is scarce. Watson (1988) considered that active, time-consuming foraging methods were responsible for low nest attendancy and high risk of nestling predation in the bateleur. However, there was no obvious indication in the present study from time-lapse photography at nests that attendancy was low in comparison with other eagles or black eagles elsewhere (Chap. 8).

Selection of certain cliff aspects by nesting black eagles was not associated with any differences in failure rate, suggesting that this factor may not be of vital importance. Avoidance of east-facing cliffs might be due to inferior flying conditions (important for birds laden with prey). Strong winds from the west and south-west may create difficult down drafts over east-facing cliffs. The preferred south-facing cliffs enjoy good flying conditions and cooler temperatures. Nest-attendancy was greatly prolonged on one sunny, north-facing nest site (Chapter 8), presumably while an adult was shading the chick from the sun.

Upper escarpment pairs enjoyed fewer nesting failures (16% attempts) than lower escarpment pairs (27% attempts), probably on account of the availability of tall inaccessible nest cliffs. But the effects of this were more than compensated for by the enhanced breeding effort of lower escarpment pairs.

*Breeding success*

The proportion of double egg clutches recorded for black eagle eyries in the present study (64%) is relatively low compared with other studies (Siegfried 1968 viz. 92%; Tarboton & Allan 1984 viz. 78%; Gargett 1990 viz. 85%). Furthermore, my observations were of lower escarpment pairs which were confirmed better breeders. Single egg clutches may be produced by females breeding for the first time (Visser 1963; Siegfried 1968), but none of the eight single egg clutches observed in the present study were laid by females in sub-adult plumage, and two of the seven females involved were suspected to be old. Alternatively, reduced clutch size in raptors might result from food shortage (Newton 1979; Jenkins & Joseph 1984).

Overall breeding effort and productivity of black eagles in the Nuweveld mountains at Beaufort West between 1986 and 1990 (61% pairs/yr; 0,46 young/pr/yr), were very similar to the corresponding figures (64% pairs/yr; 0,47 young/pr/yr) for black eagles in the Matobo Hills between 1967 and 1984 (Gargett 1990). The overall failure rates experienced by the pairs in both studies were also very similar (25% of Nuweveld attempts; 27% of Matobo Hills attempts). However, most of the Matobo failures occurred at the egg stage, and many of these cases could be attributed to human depredation; remaining losses were probably due to a healthy population of other predators in the Matobo Hills National Park: outside the park, on communal land where other predators were considered to be rare, failure rate of nesting eagles was lower (Gargett 1990). In the Magaliesberg range between 1981 and 1983, (Allan 1988), black eagles made more breeding effort (81% pairs/yr), suffered heavy failure rate (30% attempts), but still raised more chicks (0,57 chicks/pr/yr). Again, most nest failure in this study occurred at the egg stage and productivity was greatly reduced by human interference. The relatively low occurrence of nest failure at the egg stage in the present study might be due to minimal human disturbance within the KRNP.

University of Pretoria etd – Davies, R A G (1994)



Only 79% of eggs laid by the study pairs actually hatched, but inviability of eggs caused only one breeding failure (the majority of inviability occurred in double egg clutches). In the Matobo Hills by contrast, as much as 42% of single egg clutches didn't hatch (Gargett 1990). It is apparent that laying two eggs can be very advantageous to black eagle breeding success. Breeding failure at the small chick stage has already been discussed. Large chicks suffered far lower mortality, the death of the large chick from an impacted crop might have resulted from low provisioning rates at this nest (Chapter 8) and a long preceding period without food. A similar occurrence was recorded by Tuer (1969) where the chick lost weight but survived.

In other *Aquila* species, breeding can be delayed or severely disrupted by the immediate effects of adverse climatic conditions such as heavy rains (Hustler & Howells 1986) or snow storms (Phillips, Wheeler, Lockhart, McEneaney & Forrester 1990). The only instance of sudden climate-induced failure in the present study was a small chick blown out of the nest by gale-force winds. The Beaufort West region is known to experience highest average wind and gust speeds (up to 175kph) in South Africa (Milford 1987).

In compliance with most raptor studies (as reviewed by Newton 1979), there was evidence from this survey that the pairs which initiated nesting early in the season enjoyed a greater degree of nesting success. Early breeding and successful breeding was probably encouraged by richer food supplies in lower escarpment territories, and in territories with more farmland.

Peak laying during June as recorded in this study is later than that recorded (usually May) for black eagles in the Transvaal (Tarboton & Allan 1984) and in the Matobo Hills (Gargett 1990). Later breeding can be expected for most African raptors at more southerly latitudes (Maclean 1985). However, delayed breeding can also be caused by food shortage (Newton 1979), and the early breeding of pairs nesting on farmland suggests that this may be more responsible. Black eagles are known to feed on lambs of domestic stock (Boshoff *et al.* 1991; Chapters 9 & 11). Whether lambs are scavenged or killed, they comprise a highly available food supply for eagles over relatively short periods of time. This is because eagles only normally pose a threat to very small lambs, and because most non-violent lamb mortality occurs in the first few weeks after birth (see Chapter 11). So the peak lambing season in March/April would be well timed to bring local eagles into breeding condition, but it does not necessarily confer an abundant food supply later in the year. Despite the variation most young fledged just prior to the hyrax birth pulse. Fledging times of other raptors has also been noted to coincide with peak prey abundance (Olsen & Georges 1993).

Breeding effort of the study pairs was linked to the size of their territories and to the areas of certain habitats within those territories. Pairs with more bottom plains, more lower slopes, more farmland and less upper plateau made more breeding attempts. This might suggest that pairs with more alternative prey available after the hyrax decline would be more likely to breed, but this hypothesis was not reflected by a more catholic diet among more determined breeders. Neither the proportion of red rock rabbit or domestic lamb in the diet, nor the number of species taken were associated with greater breeding effort. On the contrary, pairs with a greater proportion of hyrax in their diet were those that made more effort, and there was some indication that these pairs were also



University of Pretoria etd – Davies, R A G (1994)



more successful. There is the possibility of bias here since greater amounts of prey remains were recovered after a successful breeding attempt, and hyrax remains tend to accumulate disproportionately in such collections (Chapter 9). But better breeding can be expected in black eagle territories with greater availability of their staple prey, and the significant and positive correlation between breeding effort and estimates of hyrax numbers in the territories suggests that this is so. Large areas of bottom plains, lower slopes and sometimes farmland encompassed by lower escarpment territories support good populations of hyrax as well as a wide spectrum of alternate prey leading to a stable and diverse prey base which encourages breeding. Indeed, breeding pairs with more lagomorphs in their diet proved to be better providers (Chapter 8).

Despite earlier breeding by pairs with access to large areas of farmland and with a high proportion of lamb in their diet, a link between breeding success of black eagles and the extent of farmland in their territories or the proportion of lamb in their diet could not be demonstrated statistically. It would appear that young domestic lambs are a timely food resource which can dramatically induce breeding condition in farm eagles and lead to greater breeding effort, but that later in the season the availability of this resource is reduced such that breeding outcome is more influenced by other factors such as the proportion of hyrax in the diet.

The effects of the early 1980's drought, following good rains in the late 1970's (see Chapter 2), were widespread throughout the summer rainfall regions of southern Africa and probably accounted for the observed declines in hyrax populations in many areas including the Matobo Hills where 1984 was the worst breeding season recorded for the black eagle population there (Gargett 1990). Dips in productivity of eagle populations at this time, as far afield as wedge-tailed eagles in Australia (Robertson 1987), and golden eagles in North America (Phillips *et al.* 1990), may have been caused by adverse weather conditions resulting from the far-reaching teleconnection effects (Philander 1983) of the same El Nino event. The present study was carried out during a recovery phase after major drought and it is likely that the karoo biota were more responsive to rainfall than usual. Rock hyrax population structure was found to be very dynamic in the Karoo National Park over the study period, with recruitment and survival rates varying markedly with the timing and amounts of rainfall (Chapter 4)

Poor breeding performance might also have been expected for the Beaufort West black eagle population at the end of the hyrax population decline in 1983-84. Good rains in 1985 and to a lesser extent 1986 should have had a beneficial effect on the highly depressed hyrax population, and this may have resulted in improved eagle breeding performance as recorded for 1986. The subsequent breeding pattern (Fig. 45) suggested alternate good and poor breeding for three to four years, which may have resulted from synchronized breeding following the drought event. Breeding in alternate years is common for other large eagles where prey is less available (Skorupa 1986; Hustler & Howells 1987). Any statistical evidence of breeding in alternate years however, was probably over-shadowed by the predominance of consistently successful and consistently unsuccessful breeding pairs. This character has been recorded for black eagles elsewhere (Gargett 1990), and is a regular feature of raptor populations (Newton 1979).

A large-scale breeding effort during 1988 tallies with the highest prey capture rates recorded for this year which may have been due to high hyrax vulnerability in dry conditions as defined by a trough in summer rainfall (Chapter 8). Heavy predation in 1988 may have been partly responsible for the observed hyrax decline in that year (Chapter 12). Subsequently breeding effort appeared to be linked to prey abundance the previous December as indicated by total

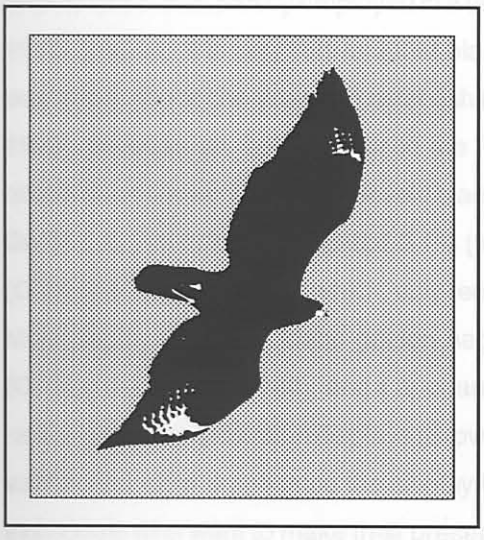
University of Pretoria etd – Davies, R A G (1994)



counts at 16 hyrax colonies within the study area (Fig. 45). It is likely that breeding should be enhanced in good prey years, but continued monitoring will reveal whether this relationship was not somewhat fortuitous. The same pattern was not evident for breeding success on account of variable failure rate. Breeding failures were minimal in 1989 when very heavy rains fell September to November, suggesting that well-timed rains may have a rapid effect on the prey base. Red rock rabbit numbers reached a peak at this time (Chapter 5). Hyrax recruitment during the study period was enhanced by early summer rains (Chapter 4). High failure rates were associated with dry conditions in the years of 1987 and 1988, but there was no obvious indication of poorer nest attendancy or reduced prey delivery rates in those years (Chapter 8).

The influence of rainfall on the breeding performance of large eagles has been found to vary between predominantly wet and dry periods. The breeding performance of tawny eagles responded positively to rain in a dry spell (presumably through effects on the prey base) but was disrupted by the immediate effects of heavy rains during the wet 1970's (Hustler & Howells 1986). Up till the late 1970's black eagle breeding in the Matobo Hills was negatively affected by heavy rains the previous season, and enhanced after dry years; in the 1980's this pattern was reversed (Gargett 1990). It has been hypothesised (Allan 1988) that during wet periods and high hyrax densities good rains actually reduce hyrax availability to black eagles by leading to increased vegetation cover and by reducing the need for hyrax to move far from rocky shelter to forage; when the hyrax population is depressed by drought however, the beneficial effects of good rains on prey abundance may lead to improved black eagle breeding performance (this aspect of the predator/prey relationship is considered in more detail in Chapter 12). As the present study was carried out during a recovery phase of the Karoo after a major drought, these effects must be borne in mind, and overall prey availability was probably a function of both changes in prey abundance and changes in prey vulnerability. However by contrast to the above studies karoo rainfall is erratic and very limiting, and it is likely that the short karoo scrub and the prey populations that it supports would always respond positively to rainfall in this water-limited environment.

*Use of space and territoriality*



Black eagles fly mainly over mountain slopes where their staple prey is most concentrated and where air currents suit their flight design. Strong updraughts over certain slopes are strategically used by flying eagles, as has been observed for golden eagles in North America (Dixon 1937). Although superior performers to other large eagles in slope lift, black eagles also soar in thermals over flat country and they must lift prey weighing as much as themselves up to their nest sites. Their unique and very characteristic wingshape is probably a compromise solution between these opposing demands of efficiency in slope lift (narrow wings), slow turning ability in thermals and the ability of generating powerful lift to get airborne with prey (broad wings).

It was easier to explain variation in the use of areas by perching eagles than that by flying eagles. This is probably because flights can be multi-purpose and are greatly influenced by weather conditions. Black eagles frequently made long ranging flights over the full extent of their ranges but they preferred to forage closer to the nest. During the nesting

University of Pretoria etd – Davies, R A G (1994)



season most prey was conveyed directly from capture site to the nest, and in this way black eagles behave as 'single-prey loaders' (Orians & Pearson 1979). Foraging nearer to the nest reduces transport costs but it is doubtful that these eagles would truly comply with the predictions of Central Place Foraging Theory and turn down rare opportunities of prey capture on the basis of prey size and distance from the nest. But there were not sufficient data to demonstrate this. Black eagles delivered even tiny prey (200-300g) to their nests if they were not too hungry themselves (and they also have the ability of dismembering large prey into transportable portions).

Black eagles allocated as much flying time (if not more), to keeping other conspecifics out of their foraging range as they did to actually harvesting prey. They also regularly used energetically-costly flapping flight to repel intruders, and risked injury by grappling and cartwheeling with persistent offenders. Territoriality is evidently of major importance in the daily activity of resident black eagle pairs, and largely essential for successful breeding. Black eagle pairs nest in close proximity for such a large eagle and often in open country, so it is not surprising that most of their 'spacing' behaviour is based on visual rather than auditory cues (olfactory communication is rare in birds). Crowned eagles and African fish eagles nest in densely vegetated habitats and make more use of vocal communication in spacing behaviour.







The highly conspicuous black and white plumage of black eagles is used to maximal advantage during their pendulum display which was mostly employed in a territorial context and sometimes to signal to mates in this and other (Gargett 1990) studies. It is very relevant that black eagles nesting at the highest recorded density probably display in this way every day of the year and establishing pairs were observed to display up to 16 times in a single day (Gargett 1990), whereas an isolated pair in the Rift Valley performed the pendulum display only once during 1013 h of observation (Rowe 1947). Nuweveld black eagles allocated 3,33% of flight time and 0,81% of daytime to this display. Golden eagles in Idaho allocated 0,1% (females) and 0,4% (males) of their day time to a similar undulation display (Collopy & Edwards 1989) which, only recently has been held to serve primarily a territorial function (Harmata 1982). Most display flights by Idaho golden eagles were conducted near the nest sites and along territorial boundaries (Collopy & Edwards 1989), and it appeared as if Nuweveld black eagles behaved likewise. Many eagles and other raptors perform undulation displays (Brown & Amadon 1968) but these other species are not as conspicuous as black eagles and most emphasise the display by shallow, rapid wing beats at each rise. This display is clearly used by individuals who want to make their presence known to other conspecifics ('a desire to be noticed'). Evolution of the conspicuous black eagle plumage indicates that crypsis has not been essential for this hunter which uses a high element of surprise to catch vulnerable prey away from refuge. Non-territorial juvenile black eagles however do possess a very cryptic plumage (Fig. 52).

University of Pretoria etd – Davies, R A G (1994)



It is not obvious why black eagle display flights were more apparent during the post-fledging period in the present study (Fig. 55). One would expect that eagle pairs would have more time available for territorial behaviour prior to breeding in May. Gargett (1990) observed the same phenomenon and thought that it might be due to observation effort or possibly to particular weather conditions prevailing at that time of the year (the formation of thermals and massive cumulus clouds) which encouraged high altitude soaring and display flights. High altitude soaring has been associated with a territorial function in other raptors (Ballam 1984). On several occasions during the present field study, black eagle pairs appeared to suddenly switch from conventional foraging behaviour within strict ranges to far-ranging, high altitude display flights which covered the entire territory and sometimes strayed across boundaries. These observations tally with Gargett's (1975) concept of a black eagle territory as an inverted cone, where overlap is greater at high altitude. But overlap in the present study was not extensive, and mostly occurred when the motive of high-flying eagles did not appear to be foraging. At such times, all neighbouring pairs would often ascend together and up to four pairs were observed to interact over the corners of their territories, so it sometimes became difficult to keep track of focal pairs. It was not clear whether this synchronised activity was triggered by the sight of neighbours as has been inferred elsewhere (Gargett 1990) and for other *Aquila* species (Brooker 1974; Collopy & Edwards 1989), or by some climatic change. Measures of flight behaviour showed very strong negative correlations with atmospheric pressure. Much of this relationship was probably due to better coverage of the pairs on low pressure days, but the correlation with perching behaviour was not as strong, and it is possible that high altitude flights were stimulated by ascending airflow which can be associated with a drop in pressure. Closer investigation will show whether this was the case.

The total ranges of neighbouring lower escarpment pairs of black eagles overlapped by less than 10% and usually followed clear, well-defined boundaries, often along topographical features as has been observed for the ranges of other raptors and birds (Watson & Miller 1971; Village 1982). Neighbours largely respected these boundaries and this must have reduced interference between pairs (which can, under very high density conditions, lead to breeding failure - Gargett 1990). Most truly aggressive behaviour (chasing and grappling) was directed at non-breeding intruders. Overlap in the foraging ranges of neighbouring pairs was further reduced on account of the eagles' preference for hunting near the nest area. These observations concur with the findings of Gargett (1975) that black eagles do defend territories. Brown (1988b) ascribed greater overlap (16%) between black eagle pairs in the Drakensberg to the difficulty of maintaining large ranges and to the presence of large areas of unpreferred habitat. Total exclusion of conspecifics is not a pre-requisite for territoriality, and on the basis that most of the overlap between Drakensberg neighbours occurred over the unpreferred habitats and may have involved non-foraging eagles (as indicated in the present study), I would argue that these eagles are still territorial.

The size of bird territories is often found to vary inversely with the density of certain desired habitat characteristics, such that most territories often contain similar total values for these commodities. In the case of wrens *Troglodytes troglodytes* it can be the area of rock faces (Cody & Cody 1972); for pileated woodpeckers *Dryocopus pileatus* it may be forest log and stump volumes or overstory canopy cover (Renken & Wiggers 1989); and for golden eagles it might be good jackrabbit habitats (Collopy & Edwards 1989). These habitat characters are all related to the food of the territory holders. In the case of black eagles, the key habitat character appears to be the extent of rocky habitats, the refuge resource for their staple prey (Gargett 1975, 1990; Brown 1988b). The total extent of lineal rock outcrops

University of Pretoria etd – Davies, R A G (1994)


(the more preferred hyrax refuge habitat - see Chapter 4) defended by black eagle pairs was astonishingly similar for the first three territories mapped which varied widely in size. The fourth territory mapped had 15% more lineal outcrops than the others, but it also had 34% less screes (less preferred habitat) so these effects may have been compensatory in terms of overall prey refuge within the territory. Quality-related compensatory effects between the extent of different habitat types in territories have been noted for wrens (Cody & Cody 1972) and golden eagles (Collopy & Edwards 1989). But the parameter which showed noticeably less variability than the number of hyrax groups across territories was the area safely accessible to hyrax from their rock outcrops. This safe feeding area is the closest measure of carrying capacity for the prey base (Chapter 12). It is tempting to conclude from this that black eagles may appraise and defend their territories on the basis of the extent of rocky habitats, which might be more easily assessed than hyrax numbers. The fixed extent of these refuge habitats might also provide the eagles with a good long-term indication of prey numbers despite the short-term fluctuations that do characterise hyrax populations (Chapters 1 & 4). This would be in keeping with Smith & Shugart's (1987) 'structural cue hypothesis'. If black eagle territories did not change with time this might be plausible. Large eagles are generally considered to maintain more stable territories than other raptors (Newton 1979), and some nest sites have a long history of use. Although there was no evidence of territory change during fieldwork in the present study an investigation of nest age and nest dispersion patterns in the KRNP did not lend any supporting evidence for long-term stability of black eagle territories in the Nuweveld Mountains, and initial observations on the marked stability of black eagle territories in the Matobo Hills between 1965 and 1972 (Gargett 1975) have not stood the test of time. Matobo territories increased from 58 to 65 between 1972 and 1977, and then declined to 37 by 1992 (Gargett 1993 unpubl.). These changes correlate with a major fluctuation in the prey base predicted by a hyrax population model (Chapter 12) using the Matobo rainfall pattern for this period, and supported by field observations (Gargett & Barry pers. comm.). This change may have been brought about by an unusual climate change, but the indication is that black eagle territories do not remain as permanent as the rocky habitats within them but do change somewhat with temporal variation in the prey base. Black eagles occupying small territories in high density hyrax habitats such as the Matobo Hills are probably more susceptible to changes in this prey base than elsewhere. The increased demand for both foraging time and territorial behaviour must lead to conflict at low prey density. It is not clear whether territories fell vacant in the Matobo because of the inability of the eagles to find sufficient food, or because of increased territorial behaviour by neighbours, or because of a combination of these factors. Gargett (1993 unpubl.) considers that poor recruitment to the population was contributory. Geographical variability in eagle territory size in relation to productivity and the prey base (e.g. Hustler & Howells 1990) is better known than temporal variability. It is clear that despite pronounced spacing behaviour in these long-lived eagles, territory size, as with most raptors (Newton 1979) is primarily related to food supply.

*Foraging behaviour and success*

In the literature, hunting black eagles are reputed to fly close against rock outcrops, and capture their prey by surprise. Extensive observation indicates that black eagles in the Matobo hunt their hyrax prey in just such an opportunistic manner (Gargett 1990). Although subject to certain observer bias, extensive observations in the Matobo suggested that eagles did most of their hunting late morning, early afternoon and Gargett (1990) concluded that hyrax are probably usually captured by surprise when they are basking near their rocks. Synchronicity between seasonal rhythms of hyrax and eagle foraging behaviour suggests that this does not hold true for black eagles in the Karoo. Hyrax are furthest from shelter when foraging (Chapter 4) and this is when black eagles launched most of their hunting

University of Pretoria etd – Davies, R A G (1994)



flights and made most of their strikes at prey (Figure 58). Hyrax and eagles avoid activity in the heat of the day in summer, and concentrate their activity over midday and early afternoon in winter. Tri-modal peaks in eagle activity every 3-4h may reflect motivational change in the hunter, but there was some indication that the peaks coincided with times when hyrax were most likely to initiate and terminate group foraging expeditions.

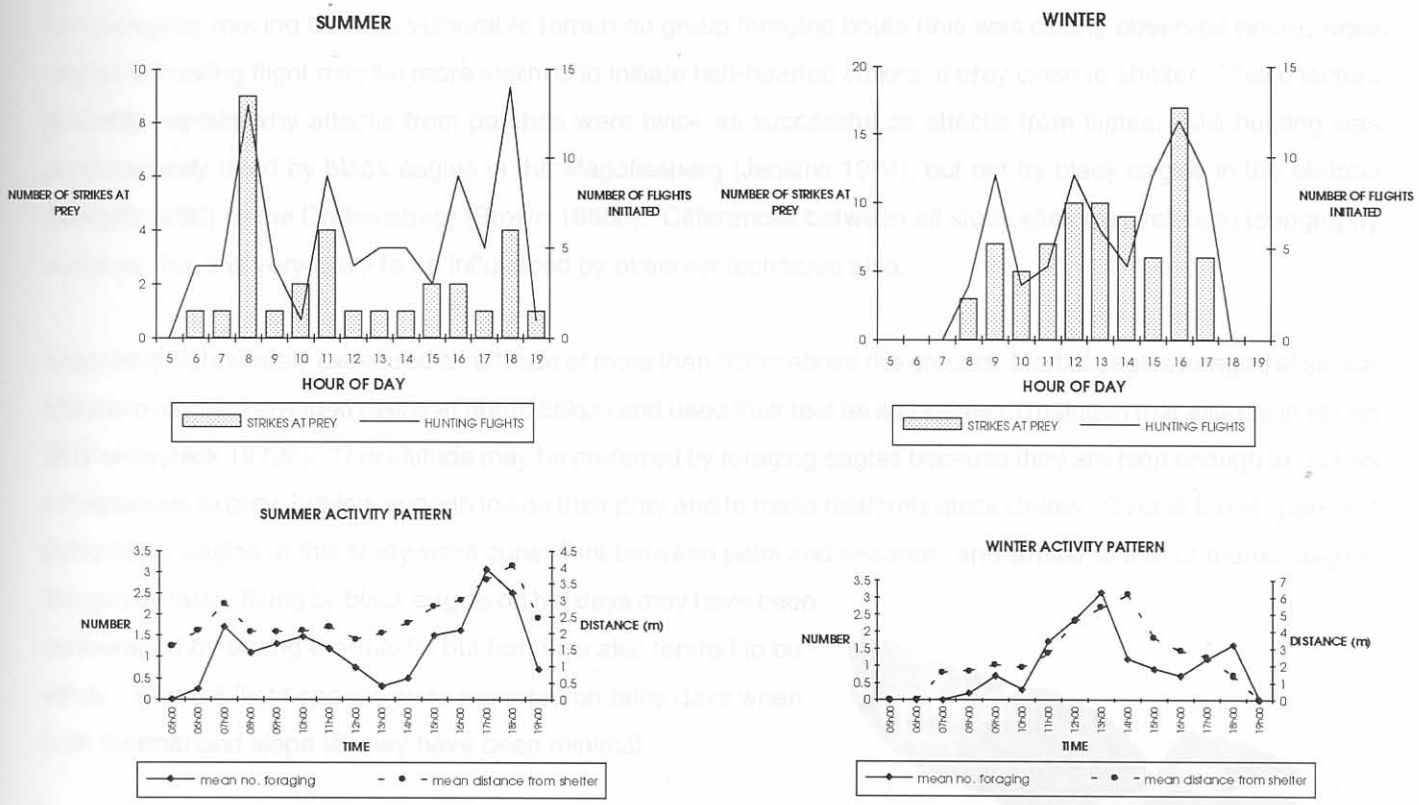



**Figure 58.** Seasonal synchronicity (summer on the left; winter on the right) in the daily foraging behaviour of black eagles (above) and hyrax (below).

The timing of hunting flights in winter correlated with patterns of mean distance from shelter that hyrax move on winter days ($r=0,57$; $p<0,05$). The timing of strikes by eagles in winter also correlated with distance from shelter ($r=0,52$; $p<0,05$) and with daily foraging pattern of hyrax in winter ($r=0,72$; $p<0,01$). Hourly statistical analysis did not confirm relationships between hyrax and eagle activity patterns in summer, but there was a tendency for eagles to launch more hunting flights at times of the day in summer when hyrax were furthest from shelter ($r=0,46$; $p=0,085$), and synchrony is evident for summer in Figure 58 although the activity peaks of hyrax and eagles may differ by an hour either way.

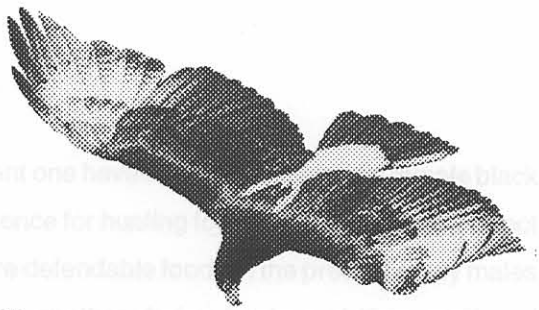
The timing of hyrax foraging behaviour is determined by other factors besides predation risk such as their need to raise their body temperature on cold winter mornings and to gather sufficient forage every day. Synchronicity in activity patterns suggests that hyrax behaviour is largely predictable in this regard and eagles can adjust their foraging behaviour accordingly although they may also face some constraints imposed by daily change in flying conditions. However the overall synchronicity may also relate to environmental factors affecting both species, and hyrax were observed to minimise synchronicity in the shorter-term, for instance during windy conditions (Chapter 4).

University of Pretoria etd – Davies, R A G (1994)



Eagles can evidently greatly increase their prey encounter rate by active hunting rather than still hunting, but at some extra energetic cost. One consequence of the flight:perch time ratio in this study was that hyrax experienced approximately equal numbers of attacks from perching and flying eagles, but this was probably fortuitous. Use of either method was evidently greatly influenced by weather conditions and motivational state of the eagles. Hyrax are probably less aware of perching eagles than flying eagles. Perching eagles may time their strikes more accurately to attack prey moving through vulnerable terrain on group foraging bouts (this was clearly observed twice), while eagles in hunting flight may be more inclined to initiate half-hearted strikes at prey close to shelter. These factors probably explain why attacks from perches were twice as successful as attacks from flights. Still hunting was predominantly used by black eagles in the Magaliesberg (Jenkins 1984), but not by black eagles in the Matobo (Gargett 1990) or the Drakensberg (Brown 1988b). Differences between all study sites may relate to topography and prey, but it is very likely to be influenced by observer technique also.

Searching flights rarely exceeded an altitude of more than 600m above the ground. Martial eagles foraged at similar altitude over the Serengeti plains at about 55kph and used their feet as air brakes to maintain that altitude in strong lift (Pennycuick 1972b). This altitude may be preferred by foraging eagles because they are high enough to be less conspicuous to prey, but low enough to see their prey and to make relatively quick strikes. Overall travel speeds of flying black eagles in this study were consistent between pairs and seasons, and similar to that of martial eagles. Marginally faster flying by black eagles on hot days may have been encouraged by strong thermal lift but hot days also tended to be windy. Slowest flight speeds were recorded on rainy days when both thermal and slope lift may have been minimal.



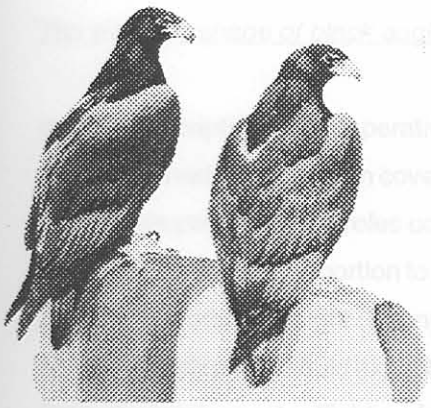
There was very little indication in the present study that black eagles flew randomly around rocky habitats in the hope of catching prey opportunistically, as has been described for black eagles hunting in the Matobo (Gargett 1990). Nearly all observed foraging behaviour involved extensive search from a high altitude perch or flight, and attacks were then launched at sighted prey. In other words, black eagles in the Nuweveld Mountains hunted by observation rather than expectation in keeping with Steyn (1982). A different approach by Matobo black eagles may be favoured in this more densely-vegetated habitat, but I would propose that hunting by expectation rather than observation is probably only successful at relatively high prey densities (such as the Matobo Hills during the 1970's), and the search hunting favoured by Nuweveld black eagles maybe in response to the difficulty in catching hyrax after a major decline in this prey base. If black eagles are hunting high density prey by expectation then time since last visit to a particular rock outcrop may be an important measure by which to judge foraging technique but it was not appropriate in the present study. Overall hunting success in the present study (8,5% of 106 strikes) was far lower than that reported for black eagles hunting in the Magaliesberg (viz. 40% of 30 strikes, Jenkins 1984) and in the Drakensberg (viz. 29% of 14 strikes, Brown 1988b). Some of this difference may have resulted from observer technique and the definition of what comprises a strike. Hunting success was not appraised in the Matobo but much greater prey capture rates in this region than in the present study (Chapter 8) indicate that hyrax were probably easier to catch during the Matobo study.

University of Pretoria etd – Davies, R A G (1994)



Both the Matobo and the present study concurred however that foraging behaviour of black eagles is highly 'state-dependent' with more flights preceding a kill and less flights thereafter. State-dependent hunting has been noted for other raptors (Mueller & Berger 1970). Much greater rates of prey capture observed in the Matobo (see Chapter 8) may have been due to greater frequency of capture opportunities while the eagles were not specifically foraging. Black eagles in the present study were catching prey approximately every other day, so days since last kill was not really a good measure for judging the motivational state of the eagles. Patterns in the foraging behaviour of black eagles are hard to evaluate because they result from a complex interaction of motivation, climate and prey density.

Whether black eagle attacks at prey are preceded by observation of the prey or not, they very often surprise the prey when approach paths are hidden from view. In the present study black eagles often used obvious tactics to conceal their approach paths from intended prey until the last seconds. Concealed attacks are more likely to be successful for prey which spend 96% of their time within five metres of shelter (Chapter 4). Obvious surprise tactics were employed by black eagles observed by Thompson (in Gargett 1990, p. 67), Brown (1988b) and Steyn (1982), but they are not always used (Gargett 1990). Hunting by surprise may have evolutionary consequences for the prey (Rudebeck 1950, 1951; Kenward 1978a). The selective nature of black eagle predation can be expected to act primarily against individuals whose behaviour places them in vulnerable situations more frequently, rather than primarily against individuals who are less well-equipped to flee. Because black eagles hunt by surprise, different components of the hyrax population should be caught in accordance with their vulnerability and not in any 'prudent' fashion (Slobodkin 1968).



Most studies, including the present one have shown that male and female black eagles have a very strong preference for hunting together, that they may select the same prey and that they share defendable food. In the present study males and females also monitored one another during hunts and they employed division of labour on nearly half of their tandem strikes and on 4/5 tandem kills. In these ways, black eagles fulfil five of the six conditions for co-operative hunting listed by Hector (1986). There was no indication that black eagle pairs used a coordinating signal during hunts, but monitoring one another may have been sufficient communication to coordinate moves. Hunting success recorded in this study provides the first indication that cooperative hunting by a large eagle may increase the success of strikes (improved success is not necessarily a pre-requisite for cooperative hunting - Bertram 1978). It is difficult to obtain sufficient data on eagle kills to demonstrate statistically significant differences in this regard. Collopy (1983a) showed that attacks by male golden eagles were twice as successful as those by females, but could not confirm this difference statistically on account of small sample size (23 kills). He could however, demonstrate that solo hunts by golden eagles were surprisingly significantly more successful than tandem hunts. Hector (1986) demonstrated that tandem hunts of bird prey by Aplomado falcons *Falco femoralis* were significantly more successful than solo hunts (37 kills), but this difference did not hold for all attacks at prey (including insects). To date, only one investigation of raptors (Harris hawks, *Parabuteo unicinctus*) has shown that cooperative foraging consistently yields improved success in attacks at prey, and more energy per individual raptor involved (Bednarz 1988).

University of Pretoria etd – Davies, R A G (1994)



Cooperative hunting by raptors, especially desert falcons chasing birds, usually takes place when the intended prey make use of vegetative cover and from which they can sometimes be flushed (Hector 1986). Raptors will generally make successive strikes at their prey and often the prey is secured after the first strike (pers. obs.). A single black eagle hunting hyrax which spend 96% of their time within 5m of refuge is unlikely to have the opportunity of repeated strikes at individual prey. By keeping close together in a tandem attack, black eagle pairs can make two strikes at the same prey in quick succession. Division of labour became apparent when prey took cover in vegetation rather than rock crevices: an adult hyrax, a juvenile hyrax, a suricate and a karoo korhaan were all taken in this situation when one bird flushed the prey at ground level and the second bird caught the prey from a 'waiting-on' position. The same approach has been observed for Aplomado falcons (Hector 1986), red-necked falcons *Falco chicquera* (Ali & Ripley 1969; Osborne 1981; Malan 1991), and black eagles catching guinea fowl (Porter 1984). A different type of cooperation has been suggested for black eagles preying on vulture chicks and hyrax, where one bird serves to distract attention from the other (Bowen 1970; Steyn 1982; Mundy, Robertson, Komen & O'Connor 1986). But the use and success of cooperative hunting (specifically division of labour) by raptors probably depends mostly on the frequency at which prey take cover in a refuge from which they can be flushed, and on the resolve of the raptors to enter that refuge. Rock hyrax may be able to avoid these situations in the Magaliesberg and the Matobo because observers did not witness division of labour by attacking black eagle pairs in these habitats (Jenkins 1984; Gargett 1990). But there was evidence to suggest that hyrax were easier to catch during both these studies, so alternatively, like search hunting, cooperative hunting may be employed more often by black eagles when prey are especially hard to catch.

*The size and shape of black eagles*

In most descriptions of cooperative hunting by raptors where division of labour was clearly apparent, the female usually flushed the prey from cover while the male waited on (Osborne 1981; Hector 1986; Malan 1991; the present study). Adoption of these roles complies with certain morphological differences between the sexes. If females are the same shape and proportion to the smaller males then one can expect a concordant increase in wing loading and power requirement in flight (Pennycuick 1972a). In the case of black eagles, females are 13% heavier than males and from scaling one would expect a 6% increase in flight area for females if they were to be the same shape as males. Proportionately greater flight surface area of females (15% greater than males) may offset greater expected wing-loading with increased mass, but this would tend to reduce agility and create more drag. This may explain why females were observed to flap more in light airs. Superior flight performance of males is offered to explain why males 'wait-on' to catch prey which is flushed by the more heavily built and powerful females.

Reversed sexual dimorphism in raptors is clearly linked to diet with raptors taking large, fast prey being more dimorphic, but the evolutionary processes behind this phenomenon are still being debated and speculated upon (see Newton 1992). I believe there are two key factors involved in this process - dispersion patterns and agility. Because males have the capacity to mate with many females whereas females are restricted to a few offspring at a time, there is a tendency for large males to arise in social animals where males can interact and dominate one another over access to females (Clark 1978). Males cannot dominate one another or monopolise harems if individuals in the population are spaced too widely by territorial behaviour related to food supplies. In many small territorial antelopes,

University of Pretoria etd – Davies, R A G (1994)



for instance, females are somewhat larger than males (see average masses for all small antelope species in Skinner & Smithers 1990). I would argue that normal sexual dimorphism cannot arise in most raptors because of their dispersion patterns. Only in the gregarious vultures is there some indication of normal sexual dimorphism (Newton 1992). In the case of carnivores, being large does not necessarily disadvantage the males in terms of hunting, but it would certainly disadvantage male raptors because of flight constraints operating against large size in birds (Pennycuick 1972a). Male raptors need to do more hunting than female raptors especially when they are provisioning food to a female with chicks. Thus one can expect stronger selection to operate on the foraging ability of males than on the foraging ability of females. Males often demonstrate their abilities to females by accelerated provisioning prior to nesting (Simmons 1989). In the case of raptors hunting elusive prey there must be strong selection forces favouring agility, and smaller birds tend to be more agile. I think this explains why males are much smaller than females in these species of raptor.

In the case of black eagles, smaller males do appear to be endowed with a more efficient and agile form for flight, and it is not surprising that when hunting as a pair the greater agility of males is used to full advantage. Despite their moderate/large size dimorphism, male and female black eagles cooperate to catch exactly the same prey, and it is relevant that males have almost as large feet as females and a longer tarsus. There were no data in the present study to suggest that the larger females captured larger prey, nor that they conveyed larger food items to the nest. Adult hyrax can weigh as much, and sometimes even more than adult black eagles. They have an extremely tough skin, a strong skeletal structure and they can be formidable adversaries. Average prey size taken by black eagles in this study was almost twice the prey size normally captured by larger golden eagles (see Chapter 8), despite the fact that golden eagles hold most of the records for the largest prey captured by eagles (see Table 26, p. 178). I suggest that disproportionately large feet in female and especially male black eagles have evolved due to specialised hunting for rock hyrax, sometimes involving cooperative behaviour.



University of Pretoria etd – Davies, R A G (1994)



Besides the observed differences in flight pattern and plumage between adult and juvenile black eagles, there were subtle differences in posture: adults generally flew on perfectly outstretched wings while juveniles often wobbled and had a hunched appearance somewhat resembling a skier on the snow slopes for the first time (see photo). High performance wings with reduced control surfaces are often unstable (Pennycuick 1972a), and the juvenile plumage of birds with such flight designs such as the bateleur (Watson 1987), and various falcons (Cramp & Simmons 1980; W. Clark pers. comm.) often endows young birds with greater control surfaces and more stability until they moult into the adult, 'high-performance' plumage. The long square tails of juvenile black eagles probably enhance stability and manoeuvrability and so assist early flying experiences. The characteristic 'leaf shape' of black eagle wings is not so evident in the juveniles - more conventional rectangular wings may assist young black eagles which are excluded from mountainous terrain by resident breeding eagles and are forced to fly great distances through more variable flying conditions over plains as well as mountains.



*Adult black eagle, possibly male, bearing down on juvenile at high speed (upper escarpment, January 1989). Note the outstretched wings of the adult and the hunched, 'survival stance' of the juvenile.*

The cryptic juvenile plumage would also assist these young birds at catching prey and evading territorial birds during a period which is normally associated with very heavy mortality in eagles (Brown 1976). Because black eagles are very long-lived and occupy territories in probably all the breeding, mountainous habitat south of the Sahara, it must be very difficult for young eagles to survive the sub-adult period and to become established as breeding adults. This scenario has been offered in explanation of the highly conservative reproductive strategy shown by black eagles, which involves obligate siblicide, and presumably results in the production of high quality offspring (Simmons 1991). In support of this hypothesis, breeding opportunities for black eagles can be expected to occur less frequently than for other species such as golden eagles which subsist on relatively less stable prey bases (see synthesis) and which show more opportunistic reproductive output (e.g. Jenkins & Joseph 1984).

University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 7*

# *DISTRIBUTION, ABUNDANCE AND FEEDING HABITS OF CARACALS AND OTHER PREDATORS*

## INTRODUCTION

The prime objective of this chapter was to collate as much information as possible about other predators besides black eagles which may be responsible for the loss of individuals from the hyrax population. The only other major predator of adult rock hyrax in the study area was the caracal, so most of the attention in this chapter is directed at this species, and some relevant general information on caracals is provided here. Initial plans to undergo a major investigation of caracal home range and movements involving radio-telemetry proved largely unsuccessful. So extensive reference is made in this chapter to other studies of caracals in similar karoo environments. Limitations on field work precluded detailed study of all predators in the KRNP, but for modelling purposes (Chapter 12) it was important to have an informed awareness of the potential impact of non-eagle predation on hyrax under more 'normal' conditions of hyrax density, and to use all the information available to try and gauge the capacity of the numerical and functional responses that these predators might show to changes in the hyrax population.

Although not as prey-specific as black eagles, caracals are considered to be an important predator of rock hyrax in the Karoo. Rock hyrax remains occurred in 7 - 9% of stomachs from caracals killed in control operations in the Cape (Pringle & Pringle 1979; Stuart 1982); in 22% of caracal scats collected in the Karoo National Park (Palmer & Fairall 1988); and rock hyrax comprised 53% of prey items identified in caracal scats collected in the Mountain Zebra National Park (MZNP) (Moolman 1984, 1986a). In the MZNP in the eastern Karoo, where black eagles may be nest-site limited (pers. obs.) and hyrax occur at high densities (Fourie 1983), caracals are considered the major hyrax predator and their relationship to this prey has been modelled mathematically (Swart *et al.* 1986).

The distribution of caracals is sympatric with that of black eagles up through the Afro-montane belt, but extends around the perimeter of the Sahara into west and north Africa, and through Arabia into Asia and India (Stuart 1984). They are not found in the equatorial forests and true deserts. At their northern limit they are considered endangered, and it is only in the Cape Province and parts of Namibia that they abound, especially in rocky terrain, and pose a threat to domestic livestock (Stuart 1984). Like black eagles, they hold a controversial position with farmers in these regions (Chapter 11), but their damage to livestock is generally considered more severe (Stuart 1981), and their role as predators of pest species such as hyrax is less well-known. Caracals are powerful predators for their size. Adult males can attain masses of up to 20 kg (Pringle & Pringle 1979). They readily kill adult antelope which may be twice their size, such as springbok and mountain reedbuck (Grobler 1981) and, unlike black eagles, are known to kill adult sheep and goats. Domestic livestock remains were found in 26 - 55% of stomachs from caracals killed in control operations in the Cape (Pringle & Pringle 1979; Stuart 1982); and comprised 23% of identifiable prey in scats collected from farmland around the MZNP (Moolman 1984, 1986b). Single caracals have been known to kill up to 21 sheep or goats in sporadic occurrences of surplus killing (Skinner 1979; Stuart 1986), and this has made them extremely unpopular with farmers.

University of Pretoria etd – Davies, R A G (1994)



Caracals are not known to be truly territorial. They are distributed in a flexible system of overlapping home ranges which in the Cape Province may vary from 15 - 56 $km^2$ for males and from 6 - 18 $km^2$ for females (Stuart 1982; Norton & Lawson 1985; Moolman 1986a, 1986b). Overlap of home ranges within the sexes is small, but a male's range may encompass those of a few females. Juvenile caracal remain in their mother's home range until independent. A female caracal becomes sexually mature at a year old; has a gestation period of 2,6 months; and may produce up to four kittens per litter at any time of the year (Stuart 1982). Up to six kittens per litter have been recorded in captivity (Kralik 1967). The flexible spatial organisation plus high propensity for population increase means that, in contrast to black eagles whose numbers are maintained relatively constant by the number of available breeding territories and by a conservative reproductive rate, caracals are able to exhibit a pronounced 'numerical' response to changes in prey density over time. The breeding potential of caracals is not much less than that of rock hyrax (Chapter 4), but hyrax can show a very rapid response to rainfall effects, so some time-lag in the numerical response by caracals might be expected.

Besides hyrax and domestic livestock, caracals are known to prey on a wide variety of other animals and can thus be considered 'generalist' predators. Early diet studies indicated that caracals fed on a range of small prey especially rodents and lagomorphs, as well as arthropods and vegetable matter (Bothma 1965; Smithers 1971; Viljoen & Davis 1973; Skinner 1979). More recent and extensive work in the Cape reveals that a range of ungulate prey, including full-grown antelope, fulfil most of caracal food needs in this region (Pringle & Pringle 1979; Grobler 1981; Stuart 1982; Moolman 1984; Palmer & Fairall 1988). Caracals are able to survive during periods of low hyrax availability in the Karoo by subsisting on these alternative prey types. It is possible that caracals may 'switch' to a diet of hyrax when these prey become super-abundant, and in this way show a 'functional' response (Holling 1959, 1965) as well as a numerical response to increases in hyrax numbers. This functional response has been shown to be of great significance in predator-prey relationships. In southern Sweden for instance, a wide variety of generalist predators which could subsist on alternate prey were able to prevent cycling in vole populations by an efficient functional response (Erlinge 1987; Erlinge, Goransson, Hansson, Hogstedt, Liberg, Nilsson, Nilsson, von Schantz & Sylven 1983; Erlinge, Goransson, Hogstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylven 1984, 1988).

There were few other predators capable of killing adult hyrax in the study area. A single pair of martial eagles hunted mostly outside of the park. Tawny eagles were not seen in the study area. Leopards *Panthera pardus* have not been seen in the area for decades, and brown hyenas *Hyaena brunnea* pass through only very rarely. Domestic dogs *Canis familiaris*, black-backed jackals and Cape foxes *Vulpes chama* were not encountered in the rocky areas around hyrax colonies, and hyrax have been known to successfully chase off adult black-backed jackals (Fourie 1983). Human predation on hyrax has not occurred in any magnitude since proclamation of the park in 1976. However, Juvenile hyrax are vulnerable to a variety of numerous, smaller 'secondary' predators in the park most notably: small grey mongoose, Cape wildcat, Cape eagle owl *Bubo capensis*, jackal buzzard *Buteo rufofuscus*, booted eagle; and possibly gymnogene *Polyboroides typus*, white-necked raven *Corvus albicollis*, Cape cobra *Naja nivea* and rock monitor *Varanus exanthematicus* (for all scientific names after first mention, see Appendix 2).

University of Pretoria etd – Davies, R A G (1994)



## METHODS

Caracals were captured in six cage traps carefully located alongside well-used game tracks. The traps were baited with varying combinations of blood, offal, feathers, and also faeces and urine sand from captive caracals (obtained from Vrolijkheid Nature Conservation Station). Trapping was organised by S. Klemm in the first half of 1988. All traps were positioned in the park, with most positions in the kloofs surrounding Stolshoek. The traps were visited every morning. When a caracal was captured, it was held against the side of the trap by moving cross-bars through the wire mesh, and given an initial intramuscular injection of Rompun (at dosages of up to 1,5 ml depending on estimated body mass) followed by a second intramuscular injection of Ketamine hydrochloride (at dosages of up to 100 mg depending on estimated body mass). The dosage of Ketamine necessary to anaesthetise the first captive caracal was much higher (125 mg for a 5 kg cat) in the absence of an administration of Rompun. The drugged cats became tractable after several minutes and were successfully anaesthetised for a couple of hours. During this time various details (sex, mass, body dimensions) were recorded, and the animals were fitted with radio collars (provided by Dr. Neil Fairall of CDNEC) which operated in the frequency range of 144,125 - 151,851 MhZ.

Throughout 1988 efforts were made to obtain two simultaneous bearings on each of the fitted transmitters from known positions in the park. This always involved two observers in radio contact from various positions overlooking the park. It was thought that previous difficulties in obtaining bearings on radio-collared caracals in the mountainous terrain (N. Fairall pers. comm.) might be overcome by conducting radio locations from the upper escarpment at 910 m above most of the park. Radio-locations of the caracals were also attempted while walking around the convoluted lower escarpment on moonlit nights.

Throughout fieldwork for the present study, scats of caracals and Cape wildcats were collected while walking around the park. Most were collected during 1987. The amount of effort spent in each habitat type in the course of fieldwork was not analysed, but all major habitats were extensively covered while plotting out rock outcrops and monitoring hyrax groups and eagle nests (Chapters 3, 4 & 6). Caracal scats were also collected while walking fixed one km transects in the various major habitat types to assess the midden densities of red rock rabbits (Chapter 5). This permitted more direct comparison between the habitats in which scats were deposited and the habitats available. The same micro-habitat variables recorded for each red rock rabbit midden (Table 7, page 67) were recorded for each caracal scat collected. Scat locations would present a biased impression of habitat selection by caracals if they were located strategically for social purposes but unlike European lynx *Lynx lynx* or Canadian lynx, caracals do not use middens and scats tend to accumulate in the areas that are used most by the cats (Grobler 1981; L.C. Moolman pers. comm.). Cape wildcat scats can be distinguished because they are smaller and usually partly or wholly buried (Palmer & Fairall 1988). Details of habitat and activity were also recorded for any direct observations of caracals and other carnivores or raptors in the course of fieldwork.

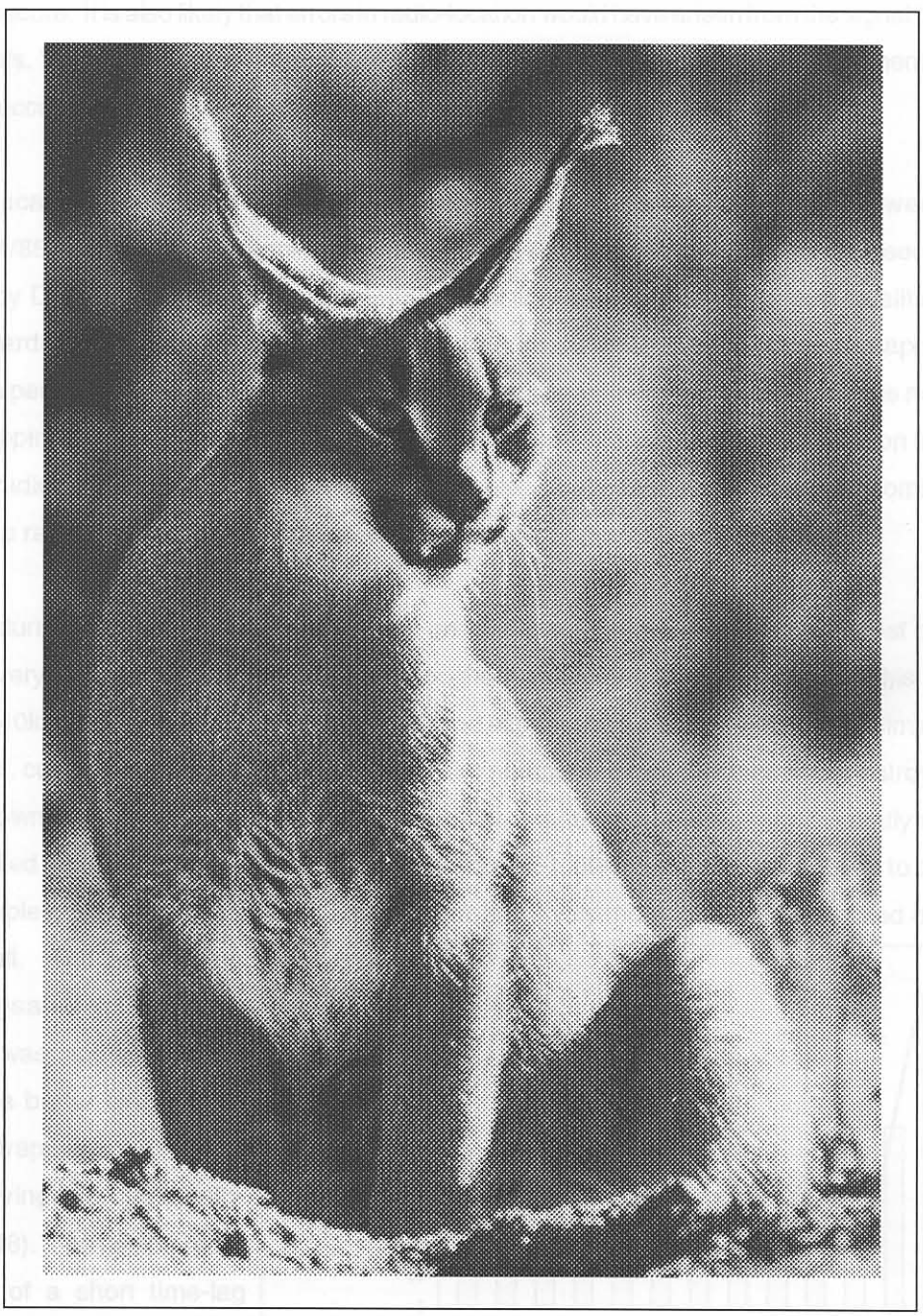
Scat analyses were carried out by G. van Dyk at the Mammal Research Institute in the following manner. Scats were initially treated using the same method as Palmer & Fairall (1988): they were dried, weighed and measured in the laboratory, and then broken apart by hand; but in the present analysis hairs were identified by taking cross sections of sample hair from each scat (after Keogh 1983), rather than using imprints of the hair (as did Palmer & Fairall 1988).

University of Pretoria etd – Davies, R A G (1994)



Using Keogh's methodology, cross section reference slides were also made up for the hair of any potential mammalian prey occurring in the KRNP which were not described in Keogh's paper (material obtained from the Transvaal Museum). Caracal diet was then expressed as percentage occurrence of each hair type in the 100 scats analysed.

Data on caracal captures in control operations were obtained from CDNEC and from private farmers in order to provide information on the relationship between numbers caught and rainfall patterns (P. Norton *in litt.*; J.H. Swiegers *in litt.*).



*Felis caracal*

University of Pretoria etd – Davies, R A G (1994)



# RESULTS

*Trapping success and radio-tracking of caracals*

Four caracals were captured and fitted with radio collars between January and May 1988. Details of these cats are provided in Appendix 4. Efforts to radio-locate these caracal were made on 17 nights, over approximately 70h. Although signals of most cats could be detected regularly from one trig. point on the upper escarpment immediately above Stolshoek (known as 'Toerentjies'), a simultaneous triangulation was only obtained on one occasion from other known localities along the upper escarpment. This was attributed to the fact that as one moves along the upper escarpment away from this trig point, the view of the convoluted terrain of the kloofs in which the cats were residing became more obscure. It is also likely that errors in radio-location would have arisen from the signal bouncing off rocky slopes in the kloofs. When efforts to radio-locate the caracals by walking along the lower escarpment on moonlit nights also proved unsuccessful, further radio-tracking efforts were discontinued at the end of 1988.

The first two caracals were captured during 349 trap nights at seven trap localities on the lower slopes between 25/1/88 and 10/4/88. This yielded a trapping success rate of 175 trap nights per caracal. The second two caracals were captured by Dirk Brand and his assistant during 172 trap nights at fourteen trap localities on the middle plateau and towards Doringhoek between 25/4/88 and 16/5/88. This latter effort yielded a trapping success rate of 86 trap nights per caracal. These workers also re-trapped one of the caracals but this was not included in the estimates of trapping success. A different area was chosen for this second trapping session in the hope that it would facilitate radio-tracking. Unfortunately this did not help. If both trapping sessions are combined, the overall trapping success rate for the KRNP in 1988 was 130 trap nights per caracal.

Trapping effort during control operations of caracal on the farm Montana near Victoria West owned by Jannie Swiegers was very intense leading up to and throughout the present study period. This farm is situated approximately 140km NNW of the present study area, and experienced a similar 3-4y cyclic climatic regime to that of Beaufort West, culminating in the drought of 1984. The numbers of caracals that were destroyed each year on this farm are shown in Figure 59 along with the total rainfall experienced each year. Evidently a high number of caracals were killed during the wet period between 1979 and 1981, but numbers killed dropped to a minimum during 1985 after a couple of very dry years. Subsequently, progressively more caracals were killed during a period of improving rainfall. The relationship between trappings and rainfall the previous summer was not statistically significant, but a better relationship emerged when trappings were compared with a moving average of rainfall (r=0,6; p=0,08). The two patterns are suggestive of a short time-lag between rainfall events and the numbers of caracals killed, which may vary from six to twelve months.

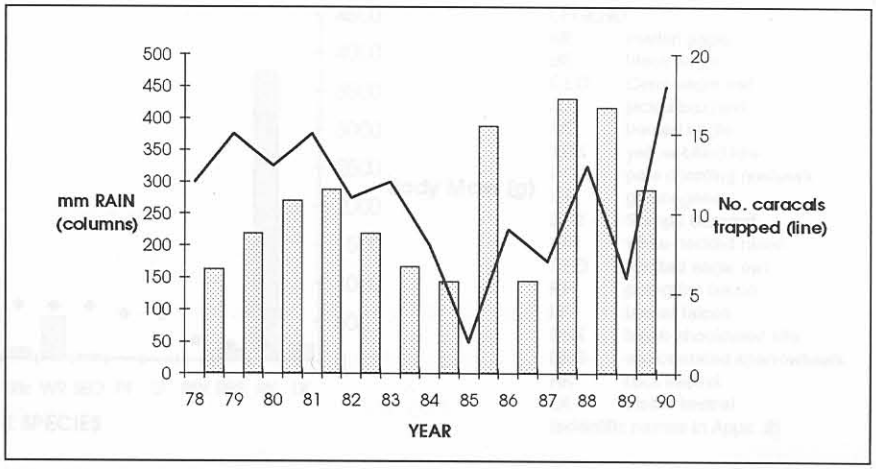



**Figure 59.** Records of the number of caracals killed in control operations on the farm Montana, near Victoria West, in relation to rainfall patterns (July to June). Data provided by J. Swiegers (*in litt.*).

University of Pretoria etd – Davies, R A G (1994)



*Relative abundance of other predators*

Relative abundance of terrestrial predators, as encountered by myself in the course of fieldwork (138 sightings), is shown in Figure 60a, in relation to average body mass. Baboons (n=84) and mongooses (n=34) were the most frequently encountered terrestrial predators (86% of sightings). Caracal sightings (n=6) slightly outnumbered Cape wildcat sightings (n=4). Most of these sightings were made during daylight.

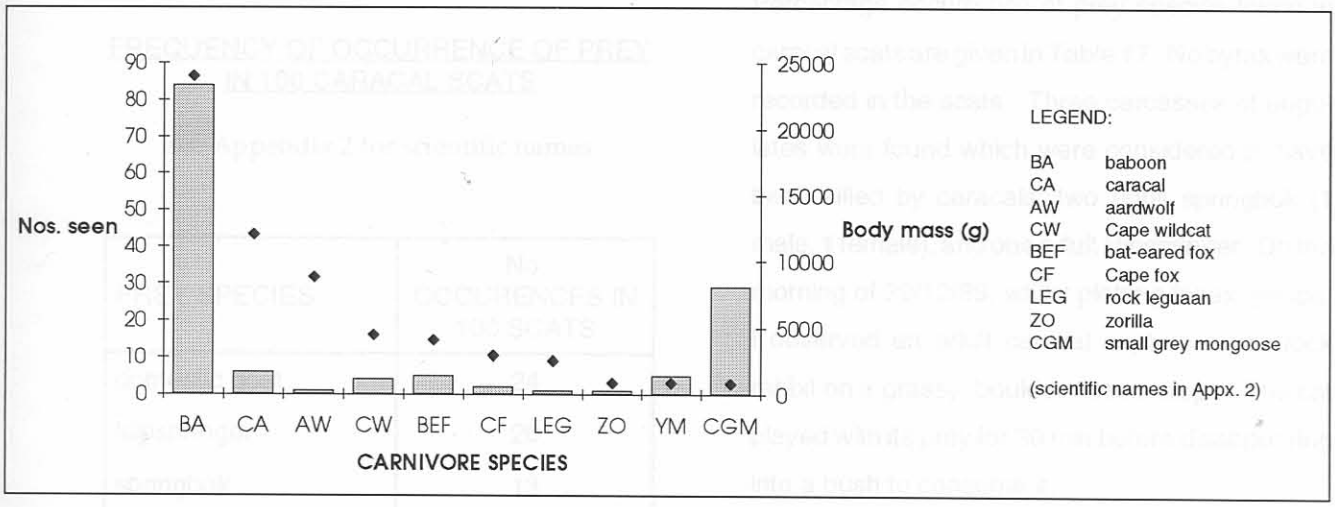



**Figure 60a.** Relative abundance of carnivores and other terrestrial predators in the KRNP, as indicated by incidental sightings of these species during fieldwork. (diamonds denote adult mass)

Relative abundance of avian predators, as encountered by myself in the course of fieldwork (783 sightings), is shown in Figure 60b, in relation to average body mass. Black eagles (n=328) and rock kestrels (n=291) comprised the bulk (79%) of these sightings. However 65% of black eagle sightings were made on routine visits to nests. Undoubtedly the frequency of these visits introduced bias into the sample. If these visits are excluded then black eagle sightings still outnumber those of all other raptors which are potential secondary predators of juvenile hyrax (booted eagles, gymnogenes, pale chanting goshawks, buzzards and white-necked ravens) at a ratio of 1,4 : 1,0. It is inferred that at least 1,5 of these smaller avian predators occur per black eagle territory (more details on raptor abundance are given under habitat selection).

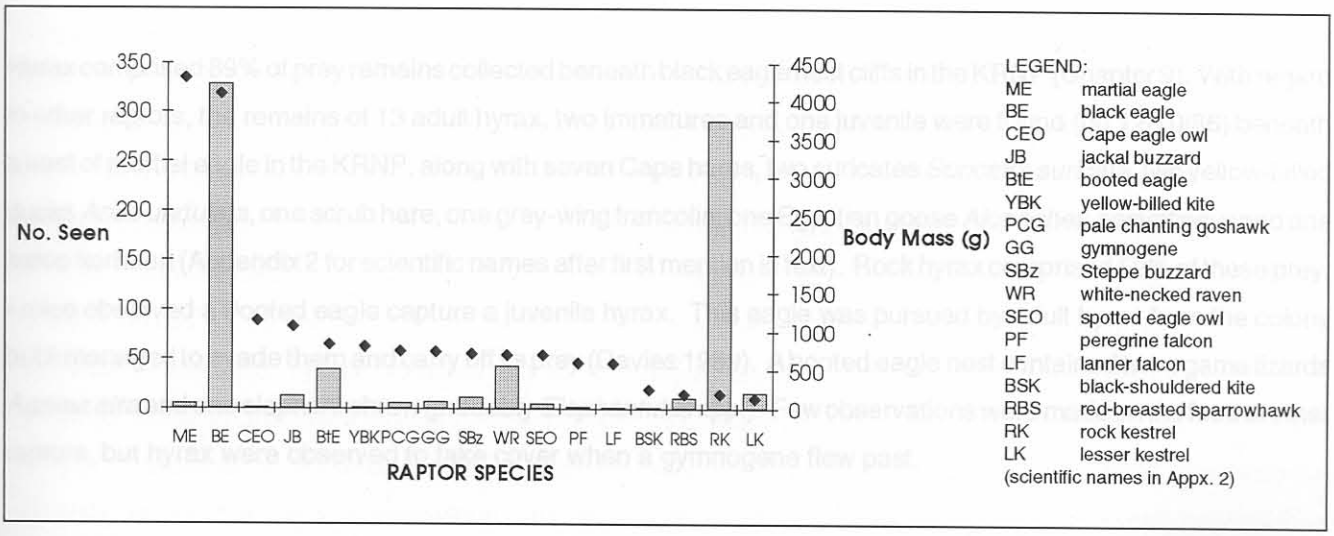



**Figure 60b.** Relative abundance of raptors and other avian predators in the KRNP, as indicated by incidental sightings of these species during fieldwork. (diamonds denote adult mass)

University of Pretoria etd – Davies, R A G (1994)



*Feeding habits*

TABLE 17

FREQUENCY OF OCCURRENCE OF PREY IN 100 CARACAL SCATS

see Appendix 2 for scientific names

| PREY SPECIES | No. OCCURENCES IN 100 SCATS |
|---|---|
| domestic goat | 24 |
| klipspringer | 20 |
| springbok | 13 |
| mountain reedbuck | 10 |
| birds | 10 |
| steenbok | 4 |
| mongoose | 3 |
| lagomorphs | 2 |
| bat-eared fox | 2 |
| grey duiker | 2 |
| ground squirrel | 1 |
| arthropods | 1 |

Percentage occurrence of prey species found in caracal scats are given in Table 17. No hyrax were recorded in the scats. Three carcasses of ungulates were found which were considered to have been killed by caracals: two adult springbok (1 male, 1 female), and one adult klipspringer. On the morning of 29/12/89, whilst plotting hyrax groups, I observed an adult caracal capture a red rock rabbit on a grassy, boulder-strewn slope. The cat played with its prey for 30 min before disappearing into a bush to consume it.

Few data were gathered on the feeding habits of other carnivores. On the morning of 16/12/87 I watched an adult Cape wildcat stalk and chase juvenile hyrax unsuccessfully. Adult hyrax fled from a Cape wildcat on another occasion. Small grey mongooses were observed to ignore juvenile hyrax even when these were isolated from their group and vulnerable. I did not observe baboons or any other potential terrestrial predators attacking hyrax.

Hyrax comprised 89% of prey remains collected beneath black eagle nest cliffs in the KRNP (Chapter 9). With regard to other raptors, the remains of 13 adult hyrax, two immatures and one juvenile were found (on 12/10/86) beneath a nest of martial eagle in the KRNP, along with seven Cape hares, two suricates *Suricatta suricata*, two yellow-billed ducks *Anas undulata*, one scrub hare, one grey-wing francolin, one Egyptian goose *Alopochen aegyptiacus* and one karoo korhaan (Appendix 2 for scientific names after first mention in text). Rock hyrax comprised 52% of these prey. I once observed a booted eagle capture a juvenile hyrax. This eagle was pursued by adult hyrax from the colony but it managed to evade them and carry off its prey (Davies 1989). A booted eagle nest contained two agama lizards *Agama atra* and one elephant shrew (probably *Elephantulus* spp.). Few observations were made on the food of other raptors, but hyrax were observed to take cover when a gymnogene flew past.

University of Pretoria etd – Davies, R A G (1994)



*Habitat selection*

Most caracal scats were recovered from the lower slopes and upper plateau. This distribution appeared to be disproportionate to the extent of these and other major habitat types (Figure 61). But the overall extent to which these habitats were sampled was not analysed. Most fieldwork was conducted on the lower slopes and middle plateau. However, transect sampling of the major habitats for red rock rabbit middens (Chapter 5) permitted comparison of caracal scat distribution with effort per habitat (Figure 62), but only 17 scats were recovered on these transects. In this analysis lower slopes were again indicated as an important caracal habitat, and middle plateau to a lesser extent. Poor scat recovery along transects on the upper slopes and plateau may have been due to taller vegetation. Few transects were conducted along the upper escarpment.

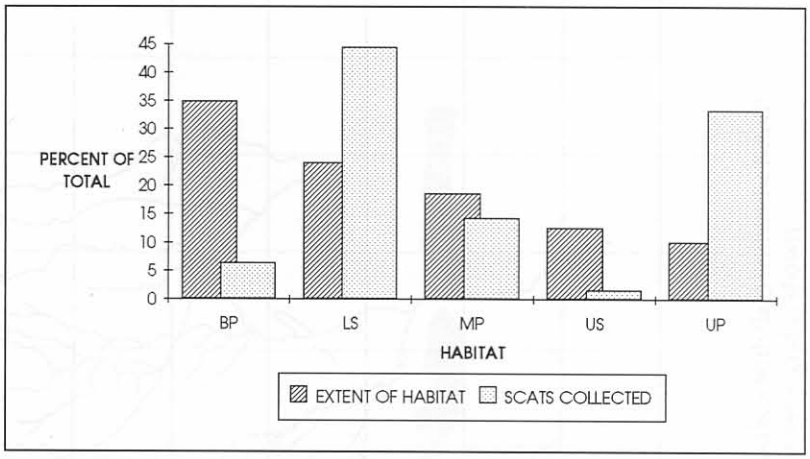



**Figure 61.** Proportional recovery of all caracal scats from the major topographical habitats in the KRNP, in relation to the proportional extent of those habitats within the park.

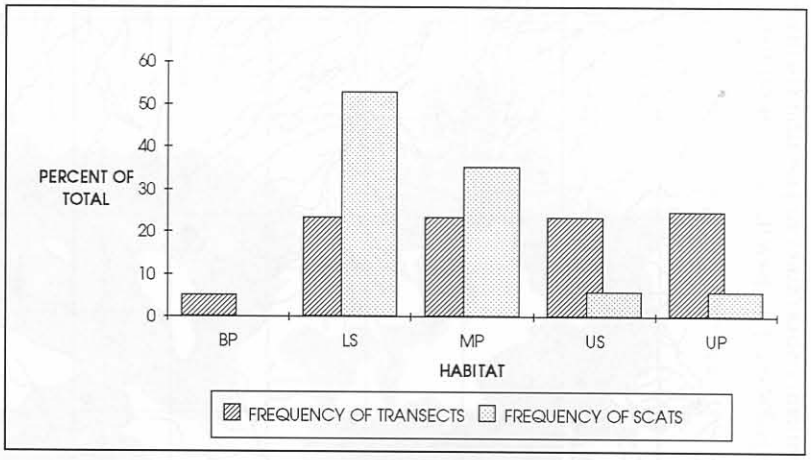



**Figure 62.** Proportional recovery of caracal scats during field transects conducted through the major topographical habitats in the KRNP, in relation to proportional sampling effort.

Many of the scats collected in the plateau habitats during the course of fieldwork were found close to the respective escarpments. This association is apparent in Figure 63 and is not likely to be entirely due to extra effort along the escarpments. On the lower slopes and valley bottoms, most caracal scats and all successful trappings were located along river courses (Figure 63). All sightings of caracals were in boulder or rocky scree habitats except one on Lammetjiesleegte (plains). Most of these sightings were either late evening (@18h30) or in the morning before 09h30, but two observations of active caracals at 11h00 and 14h45 were made on cool days. Detailed micro-habitat analyses of the limited transect data revealed some tendency for caracal scat loci to be situated closer to major rock outcrops than were habitat assessment loci, on both lower slopes ($t=-2,12$; $p<0,10$) and the middle plateau ($t=-1,82$; $p=0,10$). I could not detect any association between caracal scat loci and drainage routes or density of tall shrubs from these limited data. When compared with habitat assessment loci, caracal scat loci were associated with areas of sparser cover on the lower slopes ($t=-2,0$; $p<0,05$), and with non-grassy areas on the middle plateau ($t=-2,2$; $p=0,05$). The overall evidence suggests that caracals use all the mountainous habitats in the KRNP, especially the lower slopes; and that they tend to gravitate towards escarpment outcrops on the plateaus, and towards river courses and boulder screes in the valleys.

University of Pretoria etd – Davies, R A G (1994)

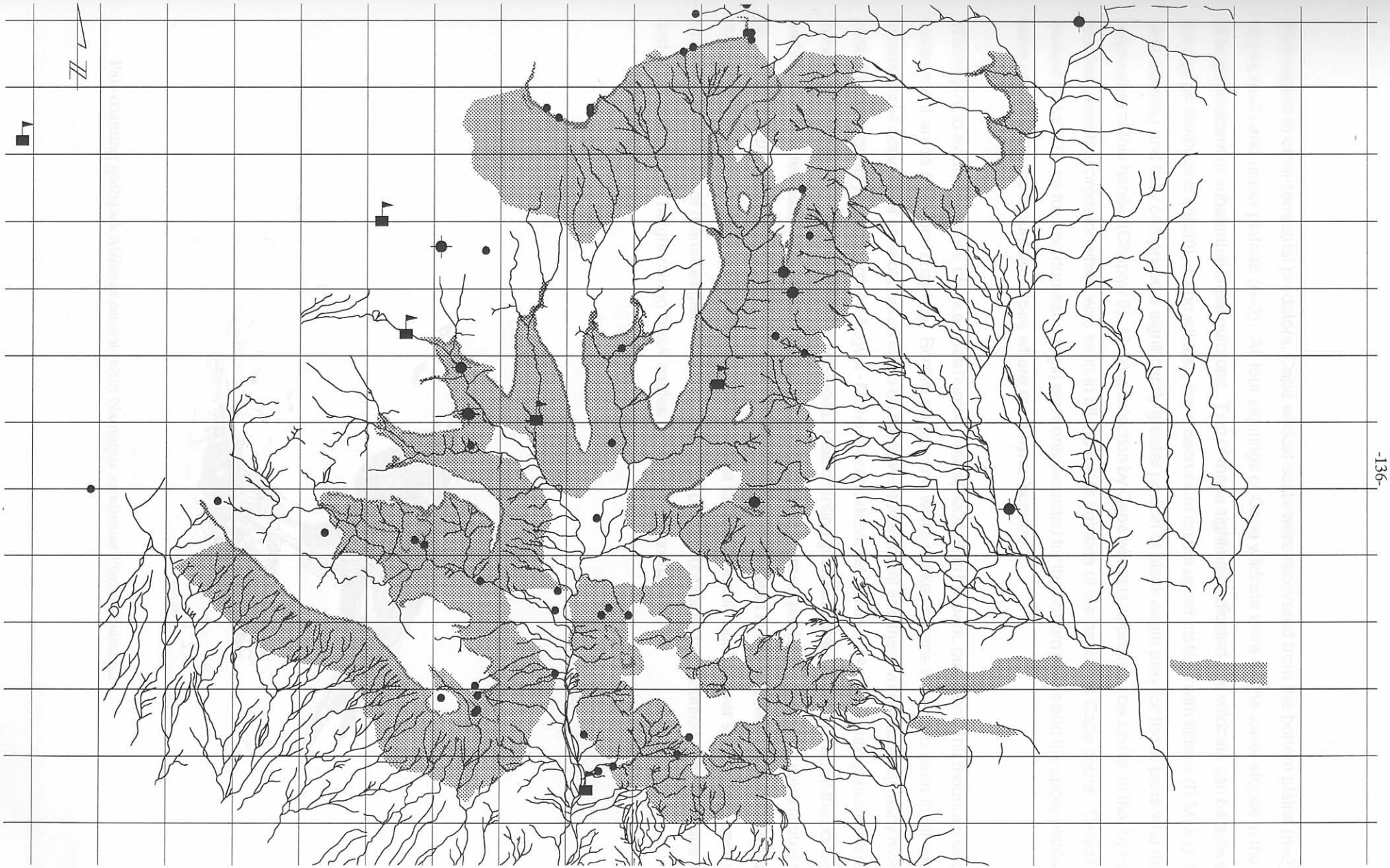


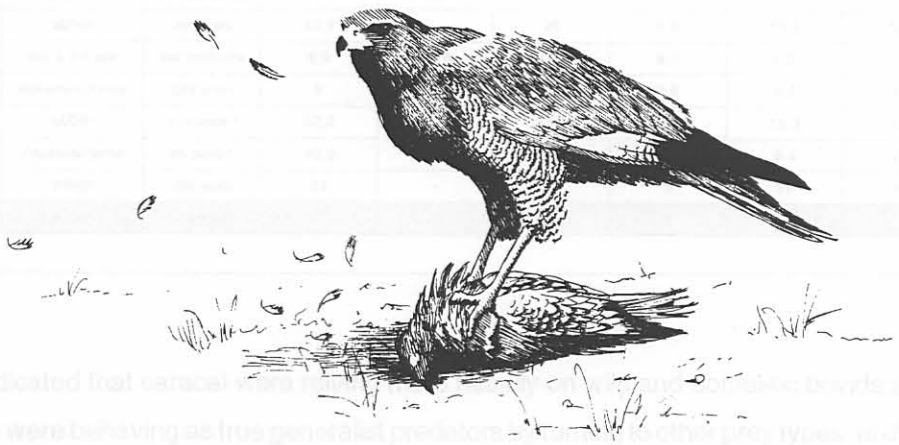
**Figure 63.** The distribution of caracal scats (small, solid circles), sightings (large, solid circles with cross pieces) and trap localities (solid box with flag) within the KRNP, in relation to episodic drainage routes (continuous lines), mountain slopes (grey) and escarpment (dark grey). One kilometer grid is shown.

University of Pretoria etd – Davies, R A G (1994)



With regard to other terrestrial predators, Cape wildcat scats were recovered from the bottom plains (n=2), lower slopes (n=2) and upper plateau (n=2). All four sightings of Cape wildcats were on the lower slopes in the vicinity of large boulders or substantial lineal outcrops. Two of these sightings indicated that wildcats can be active during the day (at 09h00 and 15h30). Cape wildcats have been seen on the upper plateau with kittens (R.M. & B. Randall pers. comm.) and they comprised a significantly greater portion of black eagle prey for those pairs who defended large areas of this habitat (Chapter 9). Habitat selection by Cape wildcats appears to be similar to that by caracals. Another terrestrial predator which was seen in all the major habitats of the park was Cape cobra. Canids (black-backed jackals, Cape fox and domestic dogs) were only recorded for the bottom plains and the upper plateau - they were not seen on the mountain slopes where most hyrax occurred.

With regard to avian predators, black eagles hunted over all habitats in the park, but mainly the mountain slopes and escarpment areas (previous chapter). Booted eagles and white-necked ravens were also seen in all habitats. I located three active nest sites of booted eagle on the lower escarpment and there were probably many more in the park. These migratory raptors arrived August - November and departed in March - April. Gymnogenes were recorded in the kloofs and along the escarpments and slopes. Pale chanting goshawks were encountered on the bottom plains and one pair was resident on the middle plateau. Jackal buzzards were surprisingly scarce and were limited to a few pairs on the upper plateau. Cape eagle owls were also only encountered in this habitat but their nocturnal habits masked any relative indication of abundance. Both these raptors probably hunted over some of the upper slopes as well. A single pair of martial eagles nested on the upper plateau but these birds hunted mostly outside the park and were excluded by neighbouring black eagles from prime hyrax habitat.



Pale chanting goshawk *Melierax canorus* with Namaqua sandrouse *Pterocles namaqua*

University of Pretoria etd – Davies, R A G (1994)



# DISCUSSION

## *Feeding habits*

Total absence of hyrax in the present analysis of caracal scats was not expected. Studies in the eastern Karoo have concluded that hyrax can comprise as much as 53% of caracal food (Grobler 1981, Moolman 1984, 1986a - see Table 18). This indicates that hyrax are not safe from caracals on account of the largely nocturnal habits of this cat. An investigation of caracal scats in the KRNP conducted three years prior to the present study recorded hyrax in 22% of scats (Palmer & Fairall 1988). Palmer (1985 unpubl.) employed feeding trials on captive caracal to compute correction factors for under- or over-estimation of prey types from scat analyses, and using various methods concluded that the observed frequency of occurrence of hyrax in caracal scats from the KRNP (22%) indicated that hyrax comprised between 12% and 29% of caracal food. Scats analysed by Palmer and Fairall were collected in 1984 when hyrax were declining from asymptotic numbers reached during the late 1970's to early 1980's, and the hyrax may have been vulnerable due to drought conditions (N. Fairall pers. comm.). The present study was conducted after the hyrax population had declined by an estimated factor of four (N. Fairall pers. comm.; Chapter 4), and the most likely explanation for the absence of hyrax as prey in the present study is that the reduced hyrax population was now well protected within its carrying capacity as defined by the extent of rocky habitat, and that the animals were simply not vulnerable to attack by mammalian carnivores. So the best indication for the relative contribution of hyrax to caracal food in the KRNP under more normal circumstances is about 20%, and it is conceivable that this might vary between 0 - 50%.

TABLE 18

COMPOSITION OF CARACAL DIET IN VARIOUS REGIONS OF THE CAPE

all values expressed as frequency of occurrence in the various sampling units, except Moolman (1984, 1986a) who expressed each value as a percentage of the total identifiable prey items

| | | | | DIET COMPOSITION | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| SOURCE | DATE | STUDY AREA | METHOD | HYRAX | DOMESTIC STOCK | WILD BOVIDS | SMALL CARNIVORES | LAGOMORPHS | RODENTS | BIRDS |
| Pringle & Pringle (1979) | 1972-75 | Bedford | 103 stomachs | 14 | 55 | - | - | - | - | - |
| Grobler (1981) | 1979-80 | MZNP | 200 scats | 53,3 | - | 20 | 0,9 | 10,6 | 5,3 | 5,3 |
| Stuart (1982) | 1980-81 | SW & E Cape | 394 stomachs | 6,8 | 27,8 | 31,4 | 5,2 | 5,2 | 9,8 | 7,4 |
| Stuart (1982) | 1980-81 | Robertson Karoo | 248 scats | 9 | 16,8 | 10,9 | 2,9 | 5,2 | 50 | 5,2 |
| Moolman (1984, 1986a) | 1982-83 | MZNP | 100 scats * | 52,5 | - | 13,5 | 5,1 | 15,3 | 8,5 | 4,3 |
| Moolman (1984, 1986a) | 1982-83 | Craddock farms | 85 scats * | 30,3 | 22,5 | 12,4 | - | 9,4 | 24 | 2,1 |
| Palmer & Fairall (1988) | 1984 | KRNP | 100 scats | 22 | - | 28 | 2 | 19 | 39 | 2 |
| Present Study (1993) | 1987 | KRNP | 100 scats | - | 24 | 50 | 5 | 2 | 1 | 10 |

The present study indicated that caracal were relying more heavily on wild and domestic bovids and birds. So it appears that caracals were behaving as true generalist predators by turning to other prey types, unlike black eagles which were successfully pursuing hyrax prey at low density (Chapter 9). Had we found a large proportion of hyrax in caracal diet, this would have been difficult to reconcile with the observation that black eagles were accounting for nearly all of the mortality of the adult hyrax age classes (Chapters 10 & 12). These findings suggest that black eagles are far more efficient at catching hyrax than are caracals. Unlike the wide-ranging black eagles which can detect

University of Pretoria etd – Davies, R A G (1994)



hyrax at great distances and cover these distances at great speed (Chapter 6), caracals must rely on stalking and ambushing their prey. A certain threshold prey density or vulnerability may be necessary for caracals to become adept at supplementing their diet with hyrax. Caracals may also be more successful predators of hyrax where black eagles are restrained by other factors such as dense vegetation or the absence of nest sites.

Red rock rabbits are an abundant potential prey species for caracals in the KRNP (Chapter 5). Having actually witnessed a caracal capture this prey, a greater reliance on lagomorphs was expected than that revealed from the present scat analyses. Lagomorphs comprised up to 15% of prey in other caracal scat studies (Table 18), and are usually underestimated in scat analyses (Palmer 1985 unpubl.). But estimation of red rock rabbit numbers in the KRNP was conducted during 1989 - 1990, and sightings of this prey in the course of fieldwork suggested a ten-fold increase in abundance from very low numbers in 1987 to a peak in 1989 (Chapter 5). Fluctuations in rabbit numbers appeared to be much more amplified than those of other prey, including hyrax. The notion that caracals were hard-pressed to catch hyrax and rabbits leading up to and during 1987 concurs with a heavier reliance on large prey items and on domestic stock as revealed by the present study. Normally, caracals in conservation areas do not kill domestic stock (see Table 18), but there was some evidence of caracals moving out into farmland from the park in the present study.

Although Cape wildcats are generally considered to be predators of murids (Skinner & Smithers 1990), and although no hyrax remains have been found in Cape wildcat scats from the KRNP (Palmer & Fairall 1988) or from the eastern Robertson Karoo (Stuart 1982), adult hyrax observed in the present study certainly perceived wildcats as a threat and young hyrax only narrowly escaped capture by this predator. It is highly likely that young hyrax are sometimes captured, especially naive animals immediately after the birth pulse. Like caracals, Cape wildcats do not appear to be strictly nocturnal, so diurnal prey are still vulnerable to them. I could find no evidence in the literature for hyrax predation by the other likely mammalian predators encountered in the present study (Cape fox, small grey mongoose, baboon). Hyrax predation by these species is probably extremely rare. Stuart (1982) recorded hyrax in 0,5% of stomachs from 114 black-backed jackals killed in control operations in the Cape. This predator was not encountered during fieldwork but has been seen occasionally on the upper plateau. Leopards are known to prey heavily on hyrax in Cape mountains (Norton, Lawson, Henley & Avery 1986) but were not present in the KRNP. The only other terrestrial predator which may pose a serious threat to at least juvenile hyrax in the KRNP (because it can pursue its prey into shelter) is the Cape cobra, but little information is available on feeding habits or density.

Black eagles and martial eagles were the only raptors encountered in the KRNP which were considered large enough to kill adult rock hyrax. Hyrax comprised 7% of prey remains collected from martial eagle nests around the Cape, and were more prevalent under cliff nests of this eagle (Boshoff, Palmer & Avery 1990). Young hyrax are recorded as prey for jackal buzzards (Steyn 1982), booted eagles (Davies 1988), pale chanting goshawks (J.H. Swiegers pers. comm.), and Cape eagle owls (on moonlit nights) although this raptor preys mostly on *Pronolagus* (Gargett & Grobler 1976; Steyn & Tredgold 1977). It is not possible to quantify the amount of the diets of these smaller raptors that is fulfilled by hyrax in the KRNP, but it is likely that all might show an immediate functional response to prey on young hyrax when these prey become super-abundant.

University of Pretoria etd – Davies, R A G (1994)



*Abundance*

Estimates of home range size for male and female caracals in the Cape are given in Table 19 along with corresponding trapping success rates and rainfall for each study area. There was no statistically significant relationship between trapping success and rainfall, so regression of density on rainfall was not enabled. By assuming non-overlapping home ranges within the sexes, and totally overlapping home ranges between the sexes, it is possible to use the values of home range size to estimate likely ranges of caracal density. I used the ratio of juvenile to adult caracals given by Grobler (1981). If caracal densities in the KRNP approached those in the S W Cape, then the average black eagle territory of 24km$^2$ should accommodate 0,48 male, 1,31 female and 1,20 juvenile caracals. If caracal densities approached those in the MZNP, then the average black eagle territory in the KRNP should accommodate 1,58 male, 4,00 female and 3,71 juvenile caracals. These extremes provide convenient, likely biological limits to the range of caracal density in the Cape. But our trapping success rate suggests that an intermediate density of approximately 1,0 male, 2,69 female and 2,47 juvenile caracals is most likely for the KRNP, and would concur with intermediate rainfall (between that in MZNP and Robertson Karoo). This prediction indicates that the KRNP (330km$^2$) might accommodate 14 male, 37 female and 34 juvenile caracals. The black eagle population in the KRNP is estimated at about 30 birds (including juveniles and non-breeders - see Chapter 6), so caracals probably outnumber black eagles at a ratio of nearly three to one.

TABLE 19

TRAPPING SUCCESS RATES AND HOME RANGE ESTIMATES FOR CARACAL IN VARIOUS REGIONS OF THE CAPE

recaptures of caracals are excluded from calculations of trapping success in all studies except Moolman (1986a & b) for the MZNP

| SOURCE | STUDY PERIOD | STUDY AREA | ANNUAL RAINFALL mm | Nos. TRAPPED | TRAP NIGHTS PER CARACAL | HOME RANGE SIZE (KM2) FEMALE | MALE |
|---|---|---|---|---|---|---|---|
| Grobler (1981) | 1979-80 | MZNP | 398 | 1 | 538 | | |
| Stuart (1982) | 1980-81 | W Cape | 237 - 1500 | 7 | 472 | 18,2 | 48,0 |
| Norton & Lawson (1985) | 1981-82 | W Cape | <1500 | 2 | 500 | 18,0 | 56,0 |
| Moolman (1986a & b) | 1982-83 | MZNP | 398 | 21 * | 90 | 5,5 | 15,2 |
| Moolman (1986a & b) | 1982-83 | Cradock farms | 398 | 13 | 146 | | 19,0 |
| Brand (1989) | 1985 | Calitzdorp | @300 | 2 | 246 | | |
| Brand (1989) | 1986 | Laingsburg | @210 | 8 | 151 | | |
| Brand (1989) | 1987 | Grahamstown | @470 | 11 | 124 | | |
| Brand (1989) | 1987 | Robertson | 237 | 9 | 121 | | |
| Fairall (in litt.) | 1984 | KRNP | 260 | 1 | @400 | | (similar MZNP) |
| Present study (1993) | 1988 | KRNP | 260 | 4 | 130 | - | - |

In 1984 Fairall (*in litt.*) and co-workers recorded greater frequencies of visits by caracals to scent posts in the Stolshoek region of the KRNP than in the recently proclaimed Doringhoek region. This difference subsequently disappeared, so it may have been caused by control operations at Doringhoek up until 1984.

University of Pretoria etd – Davies, R A G (1994)



Home range size for Cape wildcats is not known for the Cape. It is also not known for certain whether all areas of the park were used by wildcats. They may have been excluded or predated from some areas by caracal. The ratio of sightings of caracals to wildcats is the only clue available for wildcat numbers in the park. If this ratio is assumed to be representative of actual numbers (and that wildcats have a similar population structure to caracals), then the KRNP would contain about 34 adult Cape wildcats (and about 23 juveniles), and an average black eagle territory would contain about 2,5 adult wildcats (and about 1,7 juveniles). However, little confidence can be placed in these estimates and it is not possible to estimate the numbers of any other terrestrial predators in the KRNP with any certainty from available data.

*Habitat selection*

Both adult and juvenile hyrax are evidently susceptible to attack by black eagles and caracals throughout the park, and especially in their main areas of occurrence on mountain slopes. Results on habitat selection by caracals in the present study were similar to those observed by Moolman (1986a) for the MZNP, in that caracals were associated with large rocks (boulder scree) and riparian thicket. This may be due to shade-seeking behaviour and the need for cover when stalking prey. Observations in the present study are also in agreement with Moolman's (1986a) findings that caracals can be active during the day, particularly at temperatures below 22$^{o}$C. Escarpments and dry river courses probably afford convenient pathways for caracal movement and two of the caracal sightings in the present study were of animals crossing from one valley into another via a neck in the lower escarpment. Such features were found to be ideal caracal trapping sites by Brand (1989). Avoidance for grassy areas on the middle plateau and thicker plant cover on the lower slopes as indicated by the microhabitat analysis may simply be due to a preference by caracals for the less vegetated rocky areas in these habitats.

An aim of the present study of habitat selection by caracals was to predict in which areas hyrax would be vulnerable to attack by caracals, in case this might influence hyrax foraging behaviour. Hyrax are undoubtedly vulnerable to caracal attack in the vicinity of their rock outcrops, but they are probably more vulnerable when foraging away from their rocky shelters in riparian thicket. Thick vegetation along dry river courses may afford hyrax protection from black eagles, but not necessarily from attacks by caracals. It is likely that hyrax are only safe in riparian thicket over the midday period when caracals are less active (Moolman 1986a). Hyrax have an effective anti-predator strategy involving early warning and escape routes (Chapter 4). This strategy would be severely impeded in the dark, so predation by felids and owls might provide strong selective pressure opposing any development of nocturnal habits by hyrax.

Higher diversity and probably density of smaller, generalist predators such as Cape wildcat, jackal buzzard and Cape eagle owl, on the upper plateau is puzzling, but it may be due to dense vegetation supporting denser small mammal populations. Prevalence of these and other predators such as pale chanting goshawks and canids on the plateau and plains habitat types is probably not too crucial to hyrax populations, because most hyrax occur on the mountain slopes. But it is very clear that while adult hyrax face only two major enemies in the KRNP, juvenile hyrax may face **up to nine** potential predators in certain habitats.

University of Pretoria etd – Davies, R A G (1994)



*Capacity for population change*

The wide variation in numbers of caracal trapped on the farm Montana between 1978 and 1990 suggests that caracal density is very variable and that this predator might show a strong numeric response to changes in prey density. The rainfall-related pattern indicates that even intense persecution of this species does not appear to be the major influence on numbers. Caracal populations in the Cape appear particularly resilient to very heavy persecution, and numbers have actually gradually increased over the last few decades while black-backed jackal numbers have gradually declined (P. Norton *in litt.*). This indicates a very high potential for population increase. Unfortunately there are no direct data for observed rate of increase for natural caracal populations. But lines of best fit plotted through the increase and decline phases of the caracal trapping data for Montana do give some indication of the potential rate at which caracal numbers may change on Karoo farmland. While the influence of movements cannot be removed from this pattern, it at least provides some biological indication of the capacity of the numeric response on a localised basis. If it is assumed that numbers killed were directly related to numbers available, these analyses indicated a population decline at a rate of 34% per annum past a midpoint for the decline phase in July 1983, and a population increase at a rate of 22% per annum past a midpoint for the increase phase in December 1987. The drought in 1984 represented a very severe ecological event, so it is unlikely that caracal numbers would ever change much more dramatically than this. Good rains must first elicit a response in prey numbers before caracal numbers change, and a time-lag of about six months between rainfall events and caracal population response would appear appropriate for any modelling purposes.

Raptors are renowned for their ability to converge on localised irruptions of prey (e.g. Malherbe 1963). This facility enabled raptors to suppress cyclicity in vole populations in western Finland by efficient, density-dependent predation of the voles (Korpimäki 1985a, 1993). There are no data available for estimating the numeric response of generalist raptors (or other terrestrial predators) in the Karoo for modelling purposes. It is unlikely that this response would be as effective on localised hyrax irruptions as it is on rodent irruptions.

*Food requirements of the caracal population*

Estimates of the food needs of wild caracals can only be based on captive feeding trials and energetic predictions. Stuart (1982) found that eight captive caracals (mostly adult) needed an average of 586g (wet weight) meat per animal per day. This ranged from 485gd$^{-1}$ for small females to 835gd$^{-1}$ for large males. The three captive adult caracal used in Palmer's (1985 unpubl.) feeding trials consumed an average of 679gd$^{-1}$ each. Grobler (1981) monitored the food requirement of a tame but free-ranging young male caracal (weighing 11,2kg) at 796gd$^{-1}$, and predicted that a wild adult caracal would need roughly 1000g of meat per day and a wild juvenile caracal would need about 500gd$^{-1}$.

Palmer & Fairall (1988) used standard metabolic scaling (Kleiber 1961) to predict the energy requirements of a 12kg caracal at rest, and increased this estimate by 50% (after Schmidt-Nielsen 1983) for the additional energy requirements of a free-living adult caracal, to yield a figure equivalent to 3150KJd$^{-1}$. Assuming the overall energy content of meat consumed by caracals to be 22KJg$^{-1}$ dry matter (see Chapter 8), a dry matter concentration in this meat of 30% (see Chapter 8), and an assimilation efficiency for this carnivore of 80% (e.g. Golley, Petrides, Rauber

University of Pretoria etd – Davies, R A G (1994)



& Jenkins 1965; Farrell & Wood 1968; Litvaitis & Mautz 1976; Moors 1977), then in order to achieve this energy requirement of 3150KJd$^{-1}$, a wild caracal would need to consume 597g wet weight of meat per day. This is much lower than Grobler's (1981) estimate for wild adult caracal.

Nagy (1987) has shown that the field metabolic rates of wild animals are often far greater than those of captive animals, and that field metabolic rate can show a different relationship to body mass than does basal metabolic rate. This author provides various equations for estimating field metabolic rate of different groupings of animals. I used equation no. 18 for eutherians and the same assumptions on metabolisable energy content of caracal food given above to predict the food requirements of free-living male, female and juvenile caracals. The average body masses of 13,5kg for adult males and 10,5kg for adult females were calculated from data provided by Pringle & Pringle (1979) and Stuart (1982). Juvenile caracal were assumed to weigh 5kg. These data and calculations predict that in the wild an adult male caracal needs 1447g (wet weight) of meat per day; an adult female caracal needs 1179gd$^{-1}$; and a juvenile caracal needs 645gd$^{-1}$. In complete contrast to the predictions of Palmer & Fairall (1988), these predictions are far greater than those of Grobler (1981). Predictions of the food energy required by free-living black eagles using Nagy's (1987) formulae proved unrealistically high (Chapter 8), so it is possible that the predictions for caracals are also over-estimated.

Using the estimates of caracal abundance given earlier together with the predictions of field food requirements from Nagy's (1987) equation, caracals in the KRNP (330km$^2$) need to consume a total of 86kg meat (wet weight) per day or 31373kg per annum. In terms of the average black eagle territory (24km$^2$), this would correspond to an annual food consumption by resident caracals in the territory of 2282kg meat (or 1798kg if Grobler's predictions on food consumption are used). During the present study, resident black eagles only consumed about 268kg meat per territory per annum (Chapter 8). Caracals probably consume at least six times as much food as black eagles even when the eagles are catching more prey under more 'normal' conditions. In this regard, caracals can be considered more important predators overall, in this karoo environment. Caracal food consumption in a black eagle territory might vary from 1106kg if caracal numbers were as low as in the S W Cape, to 3444kg if caracal numbers were as high as in the MZNP.

*The potential impact of generalist predators on hyrax numbers*

Mean mass of hyrax in the KRNP varies from 1650g just after the birth pulse to 2430g just before it, and probably approaches 2040g overall (Chapter 4). Grobler (1981) found from feeding trials that caracals are able to consume 55% of a hyrax carcass by mass. So a 2040g hyrax carcass should yield 1122g of meat (wet weight). If, under normal circumstances, hyrax make up 20% of caracal food, then it follows from the above arguments that a standard population of caracals in the KRNP may kill up to 5600 hyrax each year. The estimated population size for hyrax in the KRNP during the study period was 13365 animals (Chapter 4) - this is after the population had declined by perhaps a factor of four (N. Fairall *in litt.*), and the population was considered to be at 60% of the local carrying capacity (Chapter 12). Palmer & Fairall (1988) estimated that caracal were consuming 420 - 460 hyrax p.a. in their study area of 120km$^2$. This would correspond to a figure of about 1210 hyrax for the present extent of the KRNP (330km$^2$). This study was

University of Pretoria etd – Davies, R A G (1994)



carried out during a major hyrax decline and so does not refer to normal conditions. Energy requirements of caracals may also have been underestimated in this calculation. Grobler (1981) estimated that caracals in the MZNP (65,4km$^2$) took an annual toll of 2995 hyrax, which would correspond to a figure of over 15000 hyrax for an area the size of the KRNP. High caracal densities and a high proportion of hyrax in the diet give rise to such a high estimate of impact which refers to a situation where hyrax probably occur at much higher density (Fourie 1983). Estimates of potential impact of caracals on hyrax populations in the Karoo are evidently variable. Predictions on caracal impact under normal conditions in this study are intermediate between other estimates of caracal impact on hyrax populations in the Karoo. Accuracy of the current assessment of impact under normal circumstances depends on three main parameters: estimated caracal density; estimated contribution of hyrax to caracal diet; and predictions of caracal food requirements. Biological field data on caracals were used in the calculation of the two former parameters but I suspect the predicted food requirements of caracals from Nagy's (1987) equation may be somewhat over-estimated, as were predicted food requirements of black eagles by this method (Chapter 8).

For comparative purposes, the consumption of hyrax by caracals in the KRNP given above would correspond to 407 hyrax killed by caracals in each black eagle territory per annum. However this scenario only portrays the impact that caracals may have on hyrax under more 'normal' conditions. During the present study hyrax numbers had declined to 1026 animals per eagle territory, caracal numbers may have been depressed, and the diet investigation indicated that they were not killing hyrax at all. It is likely though that a few were still being killed by caracals but this was undetected. Black eagles meanwhile were killing about 117 hyrax in their territories each year (Chapter 12). Under optimal conditions, caracals might conceivably increase to densities comparable to the MZNP, and they may take as much as 50% hyrax in their diet when this prey becomes super-abundant. Under such conditions, caracals have the potential to remove over 1500 hyrax from an average black eagle territory in a year. It is very unlikely that black eagles would be able to remove more than 350 hyrax from their territory in ideal conditions (Chapter 8). If the preceding assumptions and predictions are realistic, then it is apparent that caracals may play a far more important role than black eagles as hyrax predators when these prey become super-abundant.

Paucity of data on the feeding habits of the smaller generalist predators precludes such specific predictions about their impact on juvenile hyrax. Within a black eagle territory, about 417 juvenile hyrax were produced each year during the study period. About 250 of these were dying in their first year, and the variable nature of this high level of juvenile mortality was held responsible by Swart *et al.* (1986) for most change in hyrax numbers in the MZNP. These authors considered that the effects of predation were secondary in importance to this one parameter. However, hyrax are at their most vulnerable to predation in their first year of life. Just to present some perspective on this: a black eagle territory in the KRNP probably accommodates 2,2 black eagles, 3,6 adult caracals, 2,4 juvenile caracals, 2,4 adult wildcats, 1,6 juvenile wildcats, 1,6 small generalist avian predators, and an unknown number of Cape cobras. Black eagles are known to catch at least 16 juvenile hyrax in their territory every year and this is probably under-estimated due to biases inherent in analyses of prey remains collections (Chapter 10). If we assume there are about six small secondary predators per black eagle territory and that each one of these is able to catch 14 juvenile hyrax per annum, then this would amount to 84 juvenile hyrax killed. This scenario excludes any potential predation of juveniles by caracals yet it still suggests that predation may be responsible for at least 40% of the juvenile mortality referred to by Swart *et al.* (1986). This just indicates that predation should not be treated separately from juvenile mortality in population models for hyrax.

University of Pretoria etd – Davies, R A G (1994)



# CONCLUSION

Analyses of caracal scats collected from the KRNP in 1987 suggest that this predator was behaving as a true generalist by not pursuing hyrax prey at low availability (unlike black eagles which are presumed to be more efficient, specialist predators on hyrax). Differences between this food study and those of other researchers can be explained in terms of changes in prey availability. Various indications suggest that caracals may pose a threat to hyrax in all habitats of the park, but especially along the escarpments and in the riparian thickets. Radio-tracking of caracals in the park was unsuccessful, but trapping success indicated densities intermediate between those in the MZNP and in the S W Cape, in keeping with intermediate rainfall. These densities were nearly three times greater than those of black eagles, and caracals may consume six times as much food as black eagles in the park. A high degree of variation in the numbers of caracals killed on karoo farmland related to rainfall patterns rather than persecution level, and suggested that caracals can show an effective numeric response (with some time-lag) to changes in prey density. While black eagles appear to be the most important hyrax predators under the current conditions of low hyrax availability, diet studies and metabolic predictions indicate that caracals have a far greater potential for removing hyrax when these prey exceed their carrying capacity as defined by the rocky habitats. Seven species of smaller, secondary predators (five avian, one carnivore, and one reptile) are also numerous in the KRNP, and along with black eagles and caracals, are probably directly responsible for a substantial component of the mortality of juvenile hyrax which has been shown to play a major role in hyrax population dynamics in the Karoo.

University of Pretoria etd – Davies, R A G (1994)

# *PREDATOR-PREY INTERACTION*



University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 8*

# *BLACK EAGLE FEEDING HABITS -*

# *1. PREY CAPTURE RATE*

## INTRODUCTION

To interpret predator-prey interactions, a simple and fundamental requirement is to know how many prey the predators are catching. A variety of methods can be used to assess prey capture rate by eagles. Many researchers have looked at the consumption of prey by hand-fed eagles (e.g. Fevhold & Craighead 1958; Brown & Watson 1964; Love 1979; Collopy 1980, 1986; Gargett 1982a; Stalmaster & Gessaman 1982). Gargett (1982a) made predictions on the number of prey taken by black eagles in the Matobo Hills from food consumption trials involving a hand-reared eagle, and provided useful data on the proportion of hyrax carcasses consumed by the eagles. Eagles are known to abstain from breeding when food is scarce (Chapter 6). So feeding studies such as these can give a useful indication of the extra cost to a resident pair of eagles for raising offspring, and to what extent hunting eagles must increase their prey capture rate during the nesting season in order to ensure successful breeding. However, food consumption rates of captive eagles will usually be lower than those of wild birds, and metabolic predictions can be used to estimate the greater food requirements in the wild (e.g. Sapsford 1984; Nagy 1987). Field studies of prey capture rate by eagles (usually derived from observations of nests or prey on nests) are less frequent (e.g. McGahan 1967; Gargett 1972; Lockhart 1976; Collopy 1980, 1983b, 1986). This is probably due to the difficulties experienced in obtaining sufficient, accurate data on prey capture rate by eagles in the field, especially when they are not breeding. The least biased method of assessing prey capture rate is undoubtedly direct observation of the hunting eagles, but as discussed later (Chapter 9), it is very difficult to obtain adequate sample sizes with this method.

Direct or indirect observations of prey deliveries to nests, potentially afford the most data on prey capture rate by raptors in the field. Such data can be used to investigate how prey capture rate varies: across years; with chick age (e.g. Geer 1981); with pairs and characteristics of their territories; with daily climatic conditions which may favour predator or prey; and with the time of day and activity rhythms. These relationships may provide additional insight to the predator-prey interaction.

In this chapter I combine information from indirect monitoring of eagle nests, from direct observations of hunting eagles, from food consumption trials of hand-fed eagles, and from metabolic predictions in order to assess the number of prey captured by black eagles and the factors that affect this prey capture rate. The findings are contrasted with other similar studies. Comprehensive and precise determination of prey capture rate was essential for assessment of the numeric impact of eagles on hyrax in Chapter 12, and realistic minimum and maximum values for prey capture rate were also needed for modelling purposes.

University of Pretoria etd – Davies, R A G (1994)



# METHODS

*Time-lapse photography*

Eleven super-8 mm cine cameras were purchased and modified to take single frames at periodic intervals after Temple (1972). Six of these cameras (4x 6v Canon 814E; 1x9v Chinon; 1x6v Minolta) had an electronic single-frame facility which greatly facilitated the modification. The cameras which consistently gave reliable results were the Canon 814E models. These cameras are also equipped with powerful zoom lenses. The single frame facility on the remaining five cameras (1x3v Canon 310XL; 1x9v Eumig Viennette 8; 1x6v Chinon 38 Pacific; 1x6v Yashika; 1x6v Sankyo) was a manual cable release and solenoids were manufactured to operate these. Agfa 100 super-8 cine film was used throughout and developed in Germany. Each film was 50 feet (15,2m) long with a normal running time of five min. Approximately 3600 frames were available on each film.

The time-lapse circuit was designed by K. Musgrave (Diginet Systems, Pretoria), and is shown diagrammatically in Appendix 5. A photo-resistor was used to switch the unit off at night. The interval between frames could be adjusted using a variable resistor. A linear regression was obtained between time interval and resistance (Appendix 5). The system was tested at a time interval of two min for 10d at a nest in 1986. But when it was observed that most prey items could remain on the nest for a few days, I decided to increase the time interval to just over 3,5 min and increase the battery amp hours to eleven. This meant that films could be changed every 17 d instead of every 10 d.

Weather-proof housing for each camera was manufactured from 5l oil cans. The top of the cans (front) was replaced with a permanently sealed piece of transparent perspex into which I cut an aperture for the camera lens and protected this with a lens hood. It was important that the photo-resistor should press against the transparent perspex in the front and not be obscured from the light. The bottom of the cans (back) was replaced with a removable piece of perspex which I sealed off with masking tape to prevent light entering through the viewfinder. This back section could be tightened against a rubber seal with wing nuts. Cameras and circuits were positioned and orientated within these containers using foam rubber and stones, and connected by wiring to motorcycle batteries outside. The electronic circuit was bound in insulation tape to prevent short-circuiting against the metal casing. I surrounded the metal cans with 14 mm softboard to insulate them from the heat of direct sunlight, and hoped that this would make the boxes less obvious to the eagles.

This system proved sufficiently weather-proof, even through heavy rain storms for the cameras with the electronic single frame facility. However, the solenoids powering the cable releases on the other cameras used far more power and were adversely affected by the position of the box (they only functioned efficiently if vertical), and by moisture entering past the lens. This system proved unreliable and mostly unsuccessful and I abandoned the use of these cameras after 1987.

Units were attached to rocks or bushes overlooking the eagle nests at distances varying from 2 - 30m. The powerful zoom lenses of the Canon 814E cameras proved very useful, but focusing through the viewfinder did not prove

University of Pretoria etd – Davies, R A G (1994)


accurate enough especially for wide aperture conditions, and I resorted to actual measurement of the distance from the nest to the lens. The lens could then be taped firmly at the correct focal distance and zoom setting for the duration of the nesting season. Aperture was automatically controlled by the cameras. The camera box could usually be attached pointing directly at the nest by wiring it firmly to masonry nails embedded in crevices and to large rocks which I placed around the housing. The anchoring had to be very secure to withstand buffeting by winds of up to 150kph, and re-arrangements deemed necessary by the local troops of baboons. A system of using mirrors on extendable tripod legs to peer over cliff edges did not prove successful because of the high winds. Suitable viewpoints for the cameras were available at nine of the ten lower escarpment nest sites, but time-lapse photography was not feasible at upper escarpment nests because of the large cliffs (80-120m) and overhangs.

Time spent checking the cameras and changing films was minimized by synchronizing the different cameras to the same renewal dates every 17 d. While replacing film and battery I recorded age of the chick, any prey on the nest and exact time of disconnection and reconnection. The camera was run at 16 frames/second mode for a short while before removing each film so that the last frames were not over-exposed. Thorough checks of all working components were necessary at each visit.

Where possible, time-lapse photography was initiated during incubation and terminated after fledging. This provided for accurate timings of hatching and fledging, but it soon became evident that the cameras only gave a comprehensive picture of feeding habits while there was a chick in the nest. Besides diet and prey capture rate, the films could also be analysed for factors affecting the timing of prey deliveries, for nest attendancy by the adults and for development of behaviour in the chick. They also provided very useful data on eagle mortalities.



Films were analysed on an 8mm viewer to provide summarized information by film; by day; by site; and by season. Detailed, frame by frame analyses for coverages of certain nestling periods were computerized by C. Wessels. For quantification of prey deliveries, prey items were identified to species if possible, and then size of the food item was estimated by two parameters: the proportion of adult mass that the individual was thought to represent (when intact); and the uneaten proportion of that individual that was delivered. Despite the tiny format of super-8 film, the images were clear enough to derive a large amount of this information. Timing of events were calculated either by running the film through a projector and making measurements with a stopwatch, or by comparing frame numbers for the events with total frames from dawn to dusk for the respective days. Cameras commenced filming approximately 35 min before sunrise and switched off about 35 min after sunset, depending on situation and weather. Exact timings of sunrise and sunset for each day of the year were obtained for the Beaufort West weather station.

The efficiency of this system at monitoring events at eagle nests was tested by conducting direct observations of nests (135 h) or of the adult pair of eagles (61 h) concurrent with time-lapse photography, and then comparing results. Three nesting pairs were observed for a total of 196h spanning 21 d while the cameras were running (see p. 187).

University of Pretoria etd – Davies, R A G (1994)



*Direct observations*

The hunting behaviour of four resident pairs of black eagles was directly observed for eight five-day sessions during the study period. The methodology of these observations was described in detail in Chapter 6. Several days were also spent watching the nests of two other pairs during the nestling stage. Although hunting eagles were not in sight all of the time and only a portion of kills were actually witnessed, unseen kills could usually be inferred when eagles appeared with obvious, bulging crops indicating that they had just fed. This must be the least biased method for field determination of prey capture rate, and provided the only field indication of prey capture rate by black eagles outside of the nesting season.



*Food requirements of a hand-fed eagle*

Precise data on the food requirements of a black eagle were obtained by monitoring the food consumption of a hand-raised female eagle, Samburu, who was kept in captivity and under semi-natural conditions from 5d old until she attained adult plumage at three years. Samburu was taken from a nest in 1986 from the Magaliesberg mountains near Pretoria where two chicks had hatched and were engaged in siblicide (Gargett 1990). She was raised indoors using a black eagle puppet for feeding to avoid 'imprinting' (Jones 1981), and conveyed to the KRNP at the onset of fieldwork in 1986. After fledging she was mostly kept unrestrained, 'at hack' (Woodford 1970), in the park for a period of two years during which she was still reliant on an artificial food supply. She was only observed or inferred to kill for herself on a couple of occasions. So it was possible to compare food consumption while Samburu was aviary-bound with food consumption while she flew free and exercised. It is unlikely though that her food requirements would have attained those of a wild, territorial breeding bird because there was no need for her to hunt and her movements were restricted by the presence of resident pairs on all sides. Consequently she was probably inactive for a much greater portion of her time than wild eagles normally are. Samburu was very uninhibited towards humans and her freedom was temporarily curtailed after two years when she developed a habit for chasing tourists around the park. She was eventually released in the Drakensberg in 1990.

Through the nestling stage, Samburu was fed on rodents (laboratory rats and gerbils) which were initially skinned and put through a mincer. Fur and skin were introduced to the diet at age 27d to induce pellet formation and clear the crop. From age 36d Samburu was encouraged to feed herself from whole laboratory rats. This is the age at which wild eaglets begin to feed themselves (Ellis 1979; Collopy 1980, 1984; Gargett 1990). Four to five meals were provided daily to begin with and these were steadily decreased to two meals per day towards the end of the nestling period, and to one meal per day or less thereafter. Food containers were weighed before and after each meal to assess the amount of food consumed. All pellets egested by Samburu were collected and weighed. Samburu was weighed daily before meals, and a detailed diary was kept of the ontogeny of behaviours, feathering etc.. After the nestling stage, she was fed mainly on sheep heart (with and without fat attached) and to a lesser extent on day-old chicks and rock hyrax. The food consumption of a wild-caught adult black eagle was also measured over 38d while this bird was held captive before translocation.

University of Pretoria etd – Davies, R A G (1994)



The energetic cost of raising Samburu was assessed through the nestling period. Samples of cleaned rat, gerbil, rat skin and pellets were prepared and oven-dried at 65°C for 24h to assess dry matter concentration. They were then combusted in a bomb calorimeter to determine energy content. This enabled assessment of the amount of energy ingested (and regurgitated as pellets) throughout the nestling stage. To determine assimilation efficiency, energy excreted in the faeces was assessed by collecting all excreta during three feeding trials conducted at ages 17d (for 3d), 21d (for 3d) and 48d (for 2d). Excreta were collected on pre-weighed silver foil surrounding the artificial nest. After each trial the entire foil was oven-dried, weighed and samples of excreta prepared for bomb calorimetry. The weight-gain of Samburu was also determined for each trial. Oxygen consumption of Samburu at rest was determined in a metabolic chamber during three experiments at ages 18d, 37d and 47d, but the equipment proved unreliable.



*Samburu*

*Metabolic predictions*

The energy/food needs of animals are known to be related to body mass in a predictable fashion (Kleiber 1961, 1975; Kirkwood 1981; Nagy 1987). Previously, predictions on feeding rate were based on equations which describe basal or standard metabolic rate with increments for the energy cost of additional activities. A growing body of data on water turnover of wild animals now enables researchers to base their predictions on equations which actually describe the field metabolic rate of different groups of animals. This has often been shown to be greater than expected and sometimes scales to body mass in a different fashion from basal metabolic rate (Nagy 1987). As a fourth method of determining the prey capture rate of black eagles, I use various metabolic formulae including Nagy's (1987) equation for all birds (eqn. no. 30) to predict daily energy requirements. Mean mass for black eagles was determined from a collection of museum and my own records. The number of hyrax needed to fulfil these requirements were calculated using the assimilation efficiency revealed by the feeding trials, dietary information (Chapters 9 & 10), and morphological attributes of hyrax used for similar purposes in Chapter 7, and given by Gargett (1982a).

University of Pretoria etd – Davies, R A G (1994)



# RESULTS & DISCUSSION

*A test of the effectiveness of monitoring nests by time-lapse photography*

During the 196 h of direct observation of nesting pairs while time-lapse cameras were monitoring their behaviour at the nest, observers witnessed the delivery of nine prey items. These comprised five medium-sized items (three rock hyrax, one red rock rabbit and one bird), and four small items (three juvenile rock hyrax and one juvenile viverrid/ small rodent). All time-lapse films were analysed together. An assistant double-checked my findings for 67% of the period in question and both our counts tallied. These analyses were conducted without knowledge or expectation of the prey deliveries by checking against the direct observations, so no extra effort was spent searching for prey deliveries on these sections of films. Deliveries of all five medium-sized prey items during the monitoring period were noticed on analysing the time-lapse films. However, only one of the four small prey items delivered (a juvenile rock hyrax) was noticed. The deliveries of two juvenile rock hyrax and one juvenile viverrid/small rodent were missed.

The deliveries of juvenile rock hyrax were all inferred from observations made at 3km distance from a 'late' nest in November 1987. Juvenile rock hyrax weigh 200g at birth (Millar 1971). Some errors could have occurred if the adult eagles had consumed the prey before arriving at the nest for instance. The delivery of the juvenile viverrid/small rodent was however witnessed at close range, and the observer recorded that the prey was consumed in under five minutes, and then the eagles went on to consume part of a hyrax on the nest. In this case, the prey might only have been on the nest for a single frame on the time-lapse film, and then it might easily have been obscured by the eagles. During analyses of the films, it was often necessary to repeatedly run several frames through the viewer to obtain a clear view of the prey that had been delivered. Eighty five percent of all deliveries could be identified to species (Chapter 9). Most rock hyrax and red rock rabbit prey were still visible on the nest a day after they had been delivered. The time-lapse films appeared to yield accurate estimates of the timing of nest events. The calculated timing of delivery of three prey items showed an average error of 8,3 min (s.d.=4,2 min).

A time interval of just over 3,5 min between frames is evidently frequent enough to monitor the delivery of medium and large size prey, but not frequent enough to monitor the delivery of most small prey items. In the case of juvenile rock hyrax, this should not lead to great errors because nests were monitored during the nestling period which usually spanned August, September, October and seldom extended more than a few days into November. Juvenile rock hyrax were never observed before October 28 in any year, and the majority should have been born around the median birth date estimated to be November 12 (Chapter 4).

Despite some bias against small prey items which may lead to slight under-estimation of overall prey capture rate during nesting, time-lapse photography is considered to give a very reliable indication of the rate at which medium and large-sized prey are captured by the eagles during nesting, and these prey are known to make up the bulk of black eagle food (Chapter 10). It is considered very unlikely that any medium or large-sized prey would be captured and consumed by the adult eagles without some part of it being conveyed to the nest and appearing on the time-lapse films. Time-lapse photography at nests was the only practical method for obtaining a large sample of data on prey capture rate in the field.

University of Pretoria etd – Davies, R A G (1994)



*Observations on field predation rate and biomass captured*

In total, nine black eagle nests in the KRNP were monitored by time-lapse cameras for 701 nest days between 1986 and 1989 whilst the eagles were provisioning chicks with food (prey deliveries to nests only commenced when the eaglets were hatching). An annual breakdown of the number of prey deliveries is given in Table 20. These results indicated that during the nesting season, black eagles delivered 0,55 prey per day (plus some very small items which would have been missed by the cameras), so prey deliveries at nests can be expected slightly more frequently than once every other day.

TABLE 20

ANNUAL PREY CAPTURE RATES BY BLACK EAGLES INDICATED BY TIME-LAPSE PHOTOGRAPHY AT NESTS

For each year, the number of nests monitored, number of days filming, number of prey items delivered and the proportion of these items comprised by rock hyrax is given.

| YEAR | NESTS | DAYS | ITEMS | %HYRAX | kills/day | days/kill |
|---|---|---|---|---|---|---|
| 1986 | 1 | 9.50 | 4 | - | 0.42 | 2.38 |
| 1987 | 6 | 245.20 | 121 | 73 | 0.49 | 2.03 |
| 1988 | 5 | 208.00 | 130 | 75 | 0.63 | 1.60 |
| 1989 | 5 | 238.60 | 134 | 57 | 0.56 | 1.78 |
| TOTAL | 9 | 701.30 | 389 | 68 | 0.55 | 1.80 |

The number of kills observed or inferred while eagle pairs were under direct observation are given in Table 21, with a breakdown of each observation period. Overall prey capture rate for 48d of observing breeding and non-breeding eagles in their territories and at their nests was estimated to be 0,51 kills per day. The nest observations may give a slight underestimate of prey capture rate if small prey was captured and consumed away from the nest, but these make up a small portion of the total observations. Direct observations provided the only indication of how prey

TABLE 21

PREY CAPTURE RATES BY BLACK EAGLES INDICATED BY DIRECT OBSERVATION

Where the number of kills recorded for an observation stint was uncertain, a middle figure is used to calculate kills/day (e.g. 2,5 is used for 2-3 kills). "OBS" indicates whether the eagles or their nest was the target of observations.

| PAIR | DATE | OBS | ACTIVITY | DAYS | KILLS | kills/day |
|---|---|---|---|---|---|---|
| KK | Jun-87 | eagles | non-breeding | 5 | 1 to 2 | 0.3 |
| KK | Aug-88 | eagles | incubating | 5 | 2 to 3 | 0.5 |
| PB | May-89 | eagles | non-breeding | 5 | 2 | 0.4 |
| PB | Jul-89 | eagles | incubating | 5 | 2 to 3 | 0.5 |
| subtotal without chicks | | | | 20 | 8.5 | 0.425 |
| PB | Sep-88 | eagles | chick 25d | 5 | 3 | 0.6 |
| BR | Nov-87 | eagles | chick 76d | 5 | 4 to 5 | 0.9 |
| GD | Oct-88 | nest | chick 77d | 4 | 2 | 0.5 |
| SL | Sep-89 | nest | chick 25d | 4 | 2 | 0.5 |
| LH | Nov-89 | eagles | fledgling 107d | 5 | 2 to 3 | 0.5 |
| PB | Jan-90 | eagles | fledgling 145d | 5 | 2 | 0.4 |
| subtotal with chicks | | | | 28 | 16 | 0.571 |
| **OVERALL** | | | | **48** | **24.5** | **0.51** |

University of Pretoria etd – Davies, R A G (1994)



capture rate varied in and out of the nesting season. Prey capture rate during the nesting season as determined by direct observation (0,57 prey $d^{-1}$) was only 4% higher than that determined by time-lapse photography. Black eagles provisioning chicks captured an additional 0,15 prey per day when compared with those not provisioning chicks (Table 21). This trend was not statistically significant (t=-1,46; p=0,09) but sample size was only four for the non-breeding observation periods. It is expected that breeding eagles would actually catch more prey in order to meet the extra food requirements of nestlings and fledglings, and this is important when comparing values of prey capture rate with those of other studies (nearly all of which were derived during the nesting period). The nestling and post-fledging periods of black eagles span 6,6 months (Gargett 1980, 1990), much longer than the comparable period for golden eagles (4 - 5 months, Collopy 1980, 1986). At 0,571 prey $d^{-1}$ during this period, and 0,425 prey $d^{-1}$ for the rest of the year, a breeding pair of black eagles would catch 185 prey per year. Non-breeding pairs probably catch only 155 prey per year. If 46% of pairs raise chicks (Chapter 6), then overall prey capture rate in an eagle territory may be calculated as 169 prey $pr^{-1}y^{-1}$. At a ratio of one non-breeding bird per fifteen territorial pairs (0,07 non-breeding vagrants per territory, see Chapter 6), and assuming that the prey capture rate by non-breeding individuals is half the prey capture rate of non-breeding pairs (0,21 prey $d^{-1}$), it is calculated that this component of the eagle population may account for an additional five prey per territory per annum. This would bring the total, overall prey capture rate by black eagles during the present study to 174 prey per territory per annum.

The mean mass of all prey items monitored by time-lapse photography was estimated to be 2438g. The mean mass of prey items collected beneath black eagle nests at the end of each breeding season was estimated to be 2565g, and this is a more considered figure based on a much larger sample (n=3586) (see Chapter 9). Using the latter estimate and the inference on prey capture rate from the time-lapse photography it is calculated that the biomass of prey captured by a nesting pair of eagles was 1423g$d^{-1}$. Direct observations of the eagles suggested that this varied from 1090g$d^{-1}$ when not provisioning chicks, to 1465g$d^{-1}$ when provisioning. It can be inferred that breeding pairs of black eagles catch approximately 473kg of prey each year and that non-breeding pairs catch 398kg. Overall prey biomass captured by all pairs should approach 433kg per territory per annum, with an additional 13kg of prey captured by non-breeding vagrants.



From visual estimates of the proportion of each prey item that was delivered to nests, it was calculated that 24,8% of the prey was consumed prior to delivery. Thus the 1423g of prey captured per day was represented by 1070g of prey delivered to nests. Upon delivery to nests, prey items had an estimated mean mass of 1689g and ranged from 179g for small, unidentified prey to 3570g for an entire klipspringer lamb that was estimated to be 30% of adult mass. This record implies that black eagles are able to convey prey which is almost the same mass as themselves to their nests. Normally, the portion consumed prior to delivery was greater for larger prey captured (r=0,52; p<0,01), and this would have facilitated transport. Only 15% was consumed on average from small mongooses prior to delivery, in comparison with 22% from hyrax, 30% from scrub hares and 65% from domestic lambs. The adult birds were probably responsible for all of the prey consumption which occurred before the prey was delivered to nests. But this cannot be taken as representative of the food consumption by the adults, as has been done in other studies, because adults were also observed to feed on the nest and would regularly remove prey to feed on it and then return it to the nest (in the analyses of the time-lapse films, care was taken not to double-count these particular items).

TABLE 22

PRESENT FINDINGS ON THE PREY CAPTURE RATE BY KAROO BLACK EAGLES COMPARED WITH OTHER SIMILAR STUDIES

Prey biomass is expressed in terms of the amount captured, and the amount actually delivered to nests. Scientific names: crowned eagle *Stephanoaetus coronatus*; harpy eagle *Harpia harpyja*

| SPECIES | SOURCE | KILLS/DAY | MEAN PREY MASS (g) | BIOMASS CAUGHT (g/d) | BIOMASS DELIVERED (g/d) |
|---|---|---|---|---|---|
| golden eagle | Collopy (1980, 1984) | 1.80 | 1182 | 1814 | 1417 |
| black eagle | Gargett (1972, 1980, 1990) | 1.40 | 1546 | 2164 | |
| golden eagle | Lockhart (1976) | 0.94 | 947 | 1570 | 885 |
| golden eagle | McGahan (1967) | | | 1470 | |
| various large | Brown (1955) | 0.87 | | | |
| crowned eagle | Brown (1966) | 0.60 | | | |
| black eagle | present study | 0.57 | 2565 | 1465 | 1102 |
| black eagle | Jenkins (1984) | 0.40 | | | |
| harpy eagle | Rettig (1978) | 0.29 | | | |

Numbers and biomass of prey captured and delivered to nests in the present study are compared with corresponding values for other studies and other eagles in Table 22. With the exception of Jenkins' (1984) study of black eagle foraging behaviour in the Magaliesberg, it is evident that the rate of prey capture observed in the present study was far lower than that in most other investigations of predation by *Aquila* eagles, notably Gargett's (1990) study of black eagles in the Matobo Hills. Gargett considered that an overall prey capture rate of 365 hyrax per year was applicable for breeding pairs and 292 hyrax per year for non-breeding pairs. Besides *Procavia capensis*, the Matobo Hills is home to a second smaller species of rock hyrax, *Heterohyrax brucei*. Gargett estimated a mean hyrax mass of 1546g, which is smaller than mean mass recorded for hyrax in the present study (2040g), but adult hyrax attained even greater mass in the Matobo Hills (max 4,5kg) than in the KRNP (max 3,7kg), so one cannot necessarily conclude that the greater prey capture rate of hyrax by black eagles in the Matobo was the result of smaller prey size. Gargett's observations on prey capture rate in the Matobo were conducted in 1970 when a growing hyrax population was presumed to be especially vulnerable during a dry year (Chapter 12: Figs. 107 & 131). So it seems more likely that the difference resulted from greater prey availability in the Matobo study, and Gargett's study conveniently yields an indication of maximum potential black eagle prey capture rate. Estimates of prey capture rate by the Matobo black eagles might also be slightly exaggerated if observation periods tended to coincide with peak hunting periods of those eagles (afternoon). The low prey capture rate recorded by Jenkins (1984) is surprising since high levels of hunting success (per strike) of these birds was indicative of high prey availability (see Chapter 6). But these observations (300h) were not necessarily confined to the nesting season.

University of Pretoria etd – Davies, R A G (1994)


With the exception of the Matobo black eagles, higher prey capture rates observed for *Aquila* eagles in other studies (Table 22) can mostly be explained in terms of smaller prey size. All the golden eagle studies indicated a much higher prey capture rate, but on account of the small prey captured by golden eagles (despite the fact that golden eagles hold most of the records for largest prey taken by eagles - see Chapter 11), the calculations of prey biomass captured and delivered to nests were much more comparable to those in the present study (Table 22). Golden eagles raise up to three chicks in a much shorter nestling period of 70d to attain a larger body mass (Collopy 1980, 1986), so one would actually expect their family food requirements to be much greater than those of black eagles. Although raptors should be able to increase foraging effort and thus success as needs be, many studies have shown that prey capture rate by raptors does not necessarily correspond to family food requirements and is probably more limited by prevailing foraging success (Tinbergen 1940; Snyder & Snyder 1973; Newton 1978; Collopy 1980, 1984).

The values in Table 22 mostly relate to the brood-rearing phase. There has been some indication that prey capture rate drops during the post-fledging phase of black eagles (Gargett 1972), crowned eagles (Brown 1966) and golden eagles (Collopy 1980). But prey capture rate is difficult to assess when the eagles are not nest-site bound because kills are more likely to be unseen or undetected. Daily food requirements of nestlings and fledglings are not very different (Collopy 1980), so for the purposes of calculating annual prey capture rate in this study and for the sake of simplicity I have assumed that prey capture rate during the post-fledging period is the same as that during the nestling period, and that prey capture rate during incubation is the same as that during the non-breeding period.

*Food consumption and energetic considerations*

As a nestling, Samburu was larger than most. At 10 weeks of age the eaglet weighed 3641g, as compared to 3350g for an eaglet raised by Gargett, and a mean value of 3402g for eleven wild 10-week old eaglets (Gargett 1982a). However, Samburu attained a mean post-fledging mass of 3775g which falls below the mean weight of 3969g for six female eagles from South Africa (A.C. Kemp *in litt.*; pers. rec.). The possibility exists that rapid growth of Samburu may have been encouraged by a rich food supply in captivity, and this should be borne in mind in the following interpretation.

During the nestling phase (6-94d), Samburu was fed predominantly on laboratory rats (89% of food) with the remainder being made up of smaller rodents. Three feeding experiments (Table 23) demonstrated that she achieved a very high and remarkably constant level of assimilation efficiency (87%) on this diet. Dry matter concentration and calorific content (as determined by bomb calorimetry) of food stuffs, pellets and excreta are presented in Table 24. Laboratory rats are rich in energy and yield approximately 8KJ for each gram wet weight (Bird & Ho 1976; the present study; see Tables 24 & 25). Most raptors assimilate only 75% of the energy that they ingest (Kirkwood 1981). However, only small amounts of fur were ingested in one of the trials and no pellets were regurgitated during the experiments. Stalmaster & Gessaman (1982) noted that captive bald eagles achieved high assimilation efficiency (85%) on an energy-rich duck diet, but that their assimilation efficiencies on a salmon or rabbit diet were normal (75%). Golden eagle nestlings hand-raised by Collopy (1980, 1986) had a standard assimilation efficiency of 75% on a diet of predominantly lagomorphs. There is no evidence yet which suggests that black eagles would be more or less efficient than this on a hyrax diet.

University of Pretoria etd – Davies, R A G (1994)



## TABLE 23
### RESULTS OF THREE FEEDING TRIALS ON A HAND-FED NESTLING BLACK EAGLE

(see text for details)

| | FEEDING TRIALS | | |
|---|---|---|---|
| Expmt. No. | 1 | 2 | 3 |
| Age at start (d) | 17 | 21 | 48 |
| Duration of trial (d) | 3 | 3 | 2 |
| Weight at start (g) | 1333 | 1617 | 3420 |
| Mass gain during trial (g) | 218 | 175 | 50 |
| Dry matter consumption (g/d) | 71,3 | 68,7 | 95,0 |
| Dry matter regurgitated (g/d) | 0 | 0 | 0 |
| Dry matter excreted (g/d) | 20,1 | 20,7 | 26,4 |
| Energy consumed (KJ/d) | 1654 | 1594 | 2204 |
| Energy excreted (KJ/d) | 207 | 213 | 272 |
| Energy metabolised (KJ/d) | 1447 | 1381 | 1932 |
| Assimilation efficiency (%) | 87,5 | 86,6 | 87,7 |

## TABLE 24
### DRY MATTER CONCENTRATION AND ENERGY CONTENT OF FOODSTUFFS USED AND EXCRETA PRODUCED IN THE FEEDING TRIALS OF A HAND-FED NESTLING BLACK EAGLE

(energy content expressed as KJ/g dry weight)

| | SAMPLE SIZE | WATER CONTENT (%) | DRY MATTER CONCENTRATION (%) | MEAN ENERGY CONTENT (KJ/g) |
|---|---|---|---|---|
| Skinned rat | 10 | 68,7 | 31,3 | 23,2 |
| Entire rat | 10 | 62,2 | 37,8 | 23,4 |
| Rat skin | 5 | 49,2 | 50,8 | 26,8 |
| Gerbil | 10 | 67,2 | 32,8 | 25,1 |
| Pellets | 5 | 73,2 | 26,8 | 22,0 |
| Excreta | 10 | - | - | 10,3 |

From six days old until fledging (at 94 d old), Samburu consumed 6714g (dry matter) of food with an energy content of 165106KJ. The dry weight of pellets regurgitated during this entire period was 116g with an energy content of 2561KJ. The dry weight of excreta for the same period was estimated to be 2084g with an energy content of 21464KJ. The assimilation efficiency over the nestling period was considered to be 85% after energy regurgitated as pellets had been taken into account.

University of Pretoria etd – Davies, R A G (1994)



Changes in the mass and the daily food consumption of Samburu are shown for the entire 'dependent' period in Figure 64. This encompasses ages 0-94d as a nestling and ages 95-200d as a post-fledging 'dependent' (after Gargett 1980 & 1990 for wild eaglets). Maximum daily food consumption as a nestling occurred in week five near the end of a very rapid growth phase and shortly before maximum mass of 3500 - 4000g was attained. This agrees with the findings of Collopy (1980, 1986) and others that eaglet food needs are greatest when they are 60-80% of adult mass. After this period, food consumption dropped until the post-fledging period when it became very erratic owing to the eaglet's ability to gorge and then fast. This ability is very adaptive for wild eaglets which sometimes must survive up to 9d without food (see later). Very low food consumption rates in weeks 20 and 27-29 were due to Samburu's resistance to a change in diet. Peaks in prey consumption were also partly due to low energy food.

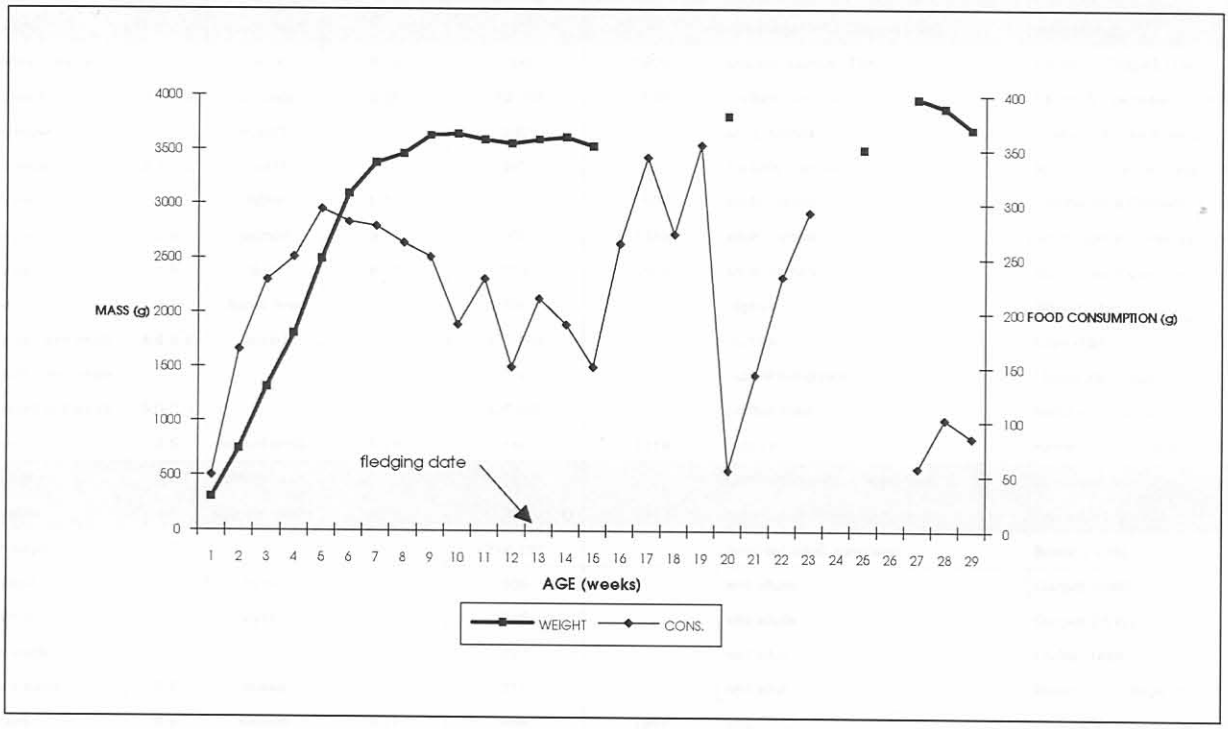



**Figure 64.** Mass gain and food consumption (wet weight) of a hand-fed juvenile black eagle during the 'dependent' period.

Other authors consider that the overall daily food requirements of nestling and fully-grown eagles are not dissimilar (McGahan 1967; Lockhart 1976; & Collopy 1980). Overall daily food consumption (wet weight) by Samburu was $218gd^{-1}$ during the nestling period on a diet of rodents, and it declined slightly to $197gd^{-1}$ during the post-fledging dependent period when she was fed predominantly on sheep heart. Values of daily food and energy consumption by black eagles in the present study are compared with those of other studies on large eagles in Table 25. The rates of food and energy consumption shown by Samburu during the post-fledging period were exactly matched by a wild-caught adult male black eagle (mass 3,7kg) which was kept in captivity for 38d. Despite increasing amounts of exercise and declining temperatures, the food consumption of Samburu dropped slightly in the 107d following the post-fledging dependent period when she was fed 80% sheep heart (Table 25).

University of Pretoria etd – Davies, R A G (1994)



# TABLE 25
## DAILY FOOD AND ENERGY CONSUMPTION OF EAGLES ON VARIOUS DIETS IN THIS AND OTHER STUDIES

(see text for details)

| EAGLE SPECIES | EAGLE MASS (kg) | DIET | FOOD ENERGY CONTENT (KJ/g wet) | DAILY FOOD CONSUMPTION (g/d wet) | DAILY ENERGY CONSUMPTION (KJ/d) | NOTES | SOURCE |
|---|---|---|---|---|---|---|---|
| Black eagle | 0,1-3,7 | laboratory rats | 7,69 | 218 | 1676 | hand-fed nestling (94d) | present study |
| Black eagle | 0,1-3,8 | hyrax | | 320 | | hand-fed nestling (93d) | Gargett (1982a) |
| Golden eagle | 0,1-4 | lagomorphs | 5,13 | 395 | 2026 | nestlings, captive (70d) | Collopy (1980) |
| Golden eagle | 0,1-4 | lagomorphs | 5,13 | 329 | 1688 | nestlings, wild (70d) | Collopy (1980) |
| Black eagle | 3,8 | sheep heart | | 197 | | hand-fed post-fledging, exercised (106d) | present study |
| Black eagle | 4,2 | hyrax | | 328 | | hand-fed post-fledging, captive (105d) | Gargett (1982a) |
| Black eagle | 3,8 | hyrax | | 260 | | hand-fed subadult, captive (34d) | present study |
| Black eagle | 3,7 | sheep heart | | 197 | | wild-caught adult, captive (38d) | present study |
| Wedge-tailed eagle | 3,7 | rabbit | 5,13 | 356 | 1826 | juvenile, captive (48d) | Brooker & Ridpath (1980) |
| Golden eagle | 3,3-5,4 | ungulate | 6,20 | 188-308 | 1538 | 4 adults, captive | Fevold & Craighead (1958) |
| Golden eagle | | meat? | | 340 | | adult, captive | Fowler in Brown & Watson (1964) |
| Golden eagle | 3,7-5,2 | meat? | | 207 | | 2 adults, captive | Wood in Brown & Watson (1964) |
| Bald eagle | 4,0 | rabbit | 5,13 | 299 | 1534 | adult, captive | Stalmaster & Gessaman (1982) |
| Bald eagle | 3,9 | salmon | 3,77 | 359 | 1353 | adult, captive | Stalmaster & Gessaman (1982) |
| Bald eagle | 3,9 | duck | 8,21 | 254 | 2085 | adult, captive | Stalmaster & Gessaman (1982) |
| Bald eagle | 4,5 | fish & liver | | 336 | | captive | Stewart (1970) |
| White-tailed sea eagle | 4,8-6,9 | mixed | | 409-618 | | captive | Love (1979) |
| White-tailed sea eagle | | | | 500 | | captive full-grown | Uttendorfer (1939) |
| White-tailed sea eagle | 5,0-5,3 | | | 400-550 | | captive male | Barth in Willgohs (1961) |
| Bateleur | 2,5 | day-old chicks | 6,23 | 180 | 1116 | captive | Kirkwood & Thompson (1983) |
| Black eagle | 3,8 | sheep heart | | 183 | | hand-fed immature, exercised | present study |
| Black eagle | 3,8 | day-old chicks | 6,23 | 230 | 1433 | hand-fed immature, exercised | present study |
| Golden eagle | 3,7 | | | 214-253 | | hand-fed adult, exercised | Brown (1976) |
| Black eagle | | hyrax | | 300 | | wild adults | Gargett (1980) |
| Black eagle | | hyrax | | 385 | | wild adults | Gargett (1972) |
| Golden eagle | | | | 227 | | wild adult | Lockie (1964) |
| Crowned eagle | 3,5 | mixed | | 210 | | wild adult | Brown (1970, page 217) |
| Bald eagle | 4,5 | salmon | 3,77 | 489 | 1844 | wild | Stalmaster & Gessaman (1984) |
| White-tailed sea eagle | | mixed | | 625 | | wild adults and nestlings (8d) | Willgohs (1961) |

In fact the food consumption rate of Samburu showed greater variation with changes in diet than with changes in temperatures or amount of exercise. It increased by about 15% on a diet of day-old chicks, and by 20 - 30% on a diet of hyrax (Table 25). Food was always supplied liberally in accordance with the appetite of the bird. Unfortunately, weight changes were not determined for all these periods. Stalmaster & Gessaman (1982) also found that the food consumption of captive bald eagles differed greatly on three diets (Table 25). Raptors are expected to ingest greater quantities of energy-deficient food (Kirkwood 1981), and the highest values of daily food consumption were for the large *Haliaeetus* eagles feeding on fish, which have a high water content (Table 25). If the food consumption values in Table 25 are averaged for the large *Aquila* eagles (excluding estimates for wild birds) then it appears that these birds need about 270g of food per day (s.d.=69) for maintenance. As discussed, this amount will depend on the energy content of the food.

University of Pretoria etd – Davies, R A G (1994)



Food consumption rates by black eagles in the present study fall below this level, whereas those of black eagles studied by Gargett (1982a) fall above it. This suggests that the diets used in this study were significantly more rich in energy than the hyrax diet fed to the eagles in Gargett's (1982a) study. The total food consumption by Samburu during the dependent period (41,4kg) was 34% lower than the total food consumption by the eaglet raised by Gargett (1982a) over the same period (63,1kg), despite the fact that Samburu appeared to grow faster.

When values of food consumption in Table 25 are converted to energy consumption according to diet, the variation between studies and eagles is much reduced. The average energy consumption of all studies involving large eagles which were hand-fed indicates that such birds need just under 1700KJ per day for maintenance. The standard deviation on this mean (254) is equivalent to 15% of the mean value, whereas the standard deviation on the findings of daily food consumption was equivalent to 26% of the mean daily food consumption. For the two feeding trials in the present study where the energy content of the feed was known, values of daily energy consumed by Samburu were slightly lower than the mean value ($1684KJd^{-1}$). If it is assumed that the black eagles in Gargett's (1982a) study needed 1684KJ per day, then the rate of food consumption on a hyrax diet (@ $320gd^{-1}$) suggests that hyrax would have to contain about $5,3KJg^{-1}$ wet weight, in order to meet this requirement. Hyrax are probably only slightly richer in energy than lagomorphs. Daily consumption of hyrax by Samburu was lower than this (Table 25) but this feeding trial was relatively short (34d) and Samburu may have lost weight over this period. However, greater rates of consumption of hyrax by Samburu than of day-old chicks suggest that the energy content of hyrax is less than $6,2KJg^{-1}$ wet weight. Feeding trials of black eagles on a hyrax diet still need to be done, in conjunction with calorimetry.

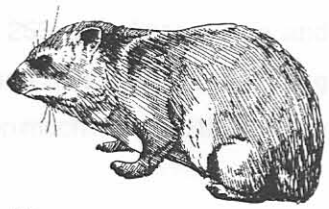
During the 34d period when Samburu's diet consisted mostly (93%) of hyrax, a total of ten small (mean mass=1086g; range 715 - 1274g) hyrax were presented to Samburu in an aviary at not less than two day intervals. Hyrax remains were collected at the end of each feeding day and weighed to assess wastage and leftovers. Samburu consumed an average of 699g from each carcass in the day (range 415 - 817g), and left approximately 42% of the carcasses by mass. The maximum amount consumed from a carcass by Samburu was not much lower than that by martial eagles which are known to consume up to 925g (Brown 1976). Crowned eagles *Stephanoaetus coronatus* are reportedly able to consume up to 1100g and golden eagles up to 1500g (Brown 1976). These records are testament to the ability of eagles to gorge themselves on large prey. Brown & Watson (1964) considered that carcass wastage by golden eagles varied between 20% and 50% depending on the size of the prey. Gargett (1982a) simulated that black eagles waste 31-37% of small hyrax, 38-49% of medium-sized hyrax, and 35-46% of large hyrax. Grobler (1981) showed that caracals waste 45% of hyrax carcasses. A wastage factor of 40% of hyrax carcasses by black eagles would appear appropriate from all these studies. This would mean that in order to achieve a consumption rate of 300g of hyrax per day, a black eagle would need to achieve an overall catch rate of about 500g of hyrax per day, or one average-sized hyrax roughly every four days.

The food consumption rates by hand-fed eagles in Table 25 cannot give a direct indication of prey capture rate in the field. Wild eagles are subject to greater energy demands than captives. Also, it is not always possible for wild eagles to catch prey at convenient regular intervals, although the effects of irregular prey capture may be buffered somewhat by the ability of eagles to gorge and lay down fat deposits. But as measures of the food and energy needed

University of Pretoria etd – Davies, R A G (1994)



by large eagles for maintenance the values in Table 25 can, however, be used to indicate a minimum prey capture rate which would at least maintain wild eagles in their territory if they were relatively inactive.



The amount of hyrax needed daily by black eagles in the feeding studies varied between about 260 - 320gd$^{-1}$. The figure of 300gd$^{-1}$ used by Gargett (1980) for food consumption by adult black eagles seems a fair approximation of food requirements on a hyrax diet, at least for maintenance (if hyrax have a food energy content of 5,5KJg$^{-1}$, this rate of food consumption would provide 1650KJ per day). To achieve this daily rate of food consumption a pair of non-breeding eagles would need to consume a minimum of 219kg of hyrax per annum. To do this the pair would need to catch a minimum of 365kg per annum. At a mean prey mass of 2565g, this would be fulfilled by a minimum prey capture rate of 142 prey per annum or 0,389 prey per day. To fulfill the additional needs of a dependent juvenile present in a breeding territory for nearly seven months in the year, the pair would need to catch and supply at least an extra 100kg of hyrax in those 200 odd days (this is based on a food consumption rate of 300gd$^{-1}$ for the juvenile). This would be fulfilled by another 39 prey of mean mass 2565g, which would necessitate an increase of the prey capture rate by 0,195 prey per day to 0,584 prey per day during the breeding season. Breeding pairs would need to catch 465kg prey per annum in order to consume 279kg. The estimate of prey biomass consumed by breeding pairs, based on direct observations of prey capture rate, was 284kg. The closeness of this value to the prediction of minimum consumption rate indicates that black eagles during the study period were operating very close to, and even below their minimum required rates of predation, and that the total energy demands of wild adult eagles cannot be much greater than the estimates of food needed for maintenance based on hand-fed individuals.

The observed prey capture rate by non-breeding eagles (0,425 prey d$^{-1}$) was actually 9% greater than the predicted minimum (0,389 prey d$^{-1}$). Whereas the observed increase in prey capture rate when provisioning juveniles (0,146 prey d$^{-1}$) was 25% lower than the predicted minimum (0,195 prey d$^{-1}$). This suggests that the food consumption rates of wild adults may be greater than 300gd$^{-1}$, while the food consumption rates of juveniles may be lower than this. The food requirements of wild adults are expected to be greater than those of hand-fed birds on a maintenance diet, because wild adults need to actively hunt and defend their territory. Wild dependent juveniles however, do not need to hunt and are usually relatively inactive (Steyn 1982; Chapter 6: Fig. 51). So it is unlikely that the food consumption rates of wild juveniles would be much greater than those of captives. In fact captive golden eagle nestlings ate considerably more than wild golden eagle nestlings (Collopy 1980: see Table 25). This is probably due to an *ad libitum* food supply in captivity, and wild black eagle nestlings may actually be able to grow healthily on less than 300g of hyrax per day. The observed increase in prey capture rate during the nesting season (0,146 prey d$^{-1}$) can be expected to yield an additional 225g food per day, but the adults may also have reduced their wastage during this period.

The estimates of total food consumption by breeding pairs of black eagles reached in the present study (279 - 284kg per annum) are lower than those determined elsewhere. Based on nest observations of prey deliveries conducted in 1970, Gargett (1972) calculated that a pair of eagles and their offspring consumed 360kg of hyrax per annum. But data on the food requirements of the young hand-fed eagle suggested an annual consumption rate of 302kg for

University of Pretoria etd – Davies, R A G (1994)



a breeding pair and their offspring (Gargett 1982a). From Brooker & Ridpath's (1980) estimate of 120kg food needed per adult bird, a total family requirement of about 330kg per annum can be inferred for a breeding pair of wedge-tailed eagles with offspring. Other estimates of annual food consumption by eagle families are lower than this: Brown & Watson (1964) calculated that a pair of golden eagles and their offspring need about 253kg food per annum; and Brown (1970) considered the family food requirements of a pair of black eagles and their chick to be 220kg consumed. It is considered unlikely though that black eagles could breed successfully on much less food than 280kg per annum (unless their diet is unusually rich in energy).

Additional food and energy requirements of wild black eagles above maintenance requirements can also be investigated by metabolic predictions based on body size. Sapsford & Mendelsohn (1984) calculated that the daily energy expenditure of free-living raptors is normally about 30% greater than their energy requirements for maintenance or existence. Drent, Ebbinge & Weijand (1978) showed that the field metabolic rate of some birds is 2,6 - 2,8 times greater than their standard or basal metabolic rate.

The mean mass of 15 South African black eagles from personal and museum records (A.C. Kemp *in litt.*) was 3819g (s.d.=419g). Mean mass for males was 3744g (n=4; s.d.=377g), and for females was 3969g (n=6; s.d.=502g). Overall representation of the sexes should be equal for black eagle families, so I use the mean mass of 3819g throughout (which is also very close to Samburu's post-fledging mass of 3775g). Some Drakensberg black eagles may, however, be much larger than this (see Brown in Gargett 1990). The standard metabolic rate of a 3819g black eagle may be calculated using the equation provided by Lasiewski & Dawson (1967) for non-passerine birds where SMR ($KCal\ d^{-1}$) = 78,3 x MASS $(kg)^{0,723}$. This equation yields a value equivalent to 863KJ $d^{-1}$ for an average black eagle. At an assimilation efficiency of 75% (Collopy 1980, 1986; Kirkwood 1981), this would require a food energy content of 1151KJ $d^{-1}$.

The energy requirement of an average black eagle for maintenance may be calculated from mean body mass using Kirkwood's (1981) equation for captive birds of prey where MEm ($KCal\ d^{-1}$) = 110 x MASS $(kg)^{0,68}$. This equation yields a value equivalent to 1145KJ $d^{-1}$ for a 3819g black eagle, requiring a food energy content of 1526KJ consumed per day (assimilation efficiency = 75%). This is only 9% lower than the mean value for large hand-fed eagles in Table 25, half of which were larger than the average black eagle. Samburu consumed 1676KJ $d^{-1}$ as a nestling, and 1433KJ $d^{-1}$ for maintenance (with some exercise) on a diet of day-old chicks.

The field metabolic rate of an average black eagle may be calculated from mean body mass using Nagy's (1987) equation No. 30 for birds where FMR ($KJ\ d^{-1}$) = 10,9 x MASS $(g)^{0,640}$. This relationship described 91% of the variation in bird FMR, but high representation of seabirds and breeding birds in the sample may lead to exaggerated FMR at large body mass. The equation yields a value of 2137KJ $d^{-1}$ for a 3819g black eagle in the wild. This value is 2,5 x greater than the figure for standard metabolic rate and 40% greater than the maintenance requirement, and would require a daily food energy content of 2849KJ (assimilation efficiency = 75%).

Using this last value for field metabolic rate and assuming that hyrax have a food energy content of 5,5KJ $g^{-1}$ wet weight, it follows that an adult pair of wild eagles would need to consume 1036g of hyrax per day, which in turn means

University of Pretoria etd – Davies, R A G (1994)



they would need to catch 1727g of hyrax per day (40% wasted). At a mean prey mass of 2565g, this corresponds to a prey capture rate by the pair of 0,673 prey $d^{-1}$ which is far larger than the observed prey capture rate of a non-breeding pair (0,425 prey $d^{-1}$), and even larger than the observed rate when breeding (0,571 prey $d^{-1}$).

If, as Sapsford & Mendelsohn (1984) suggest, field metabolic rate of an average black eagle is taken as only 30% greater than the maintenance or existence requirement predicted from Kirkwood's (1981) equation, this would indicate a daily food consumption rate of 360g $bird^{-1}$, and a daily catch rate of 1203g $pair^{-1}$ (same reasoning as above). This corresponds to a prey capture rate of 0,469 prey $d^{-1}$, which is more compatible but still greater than the observed rate and indicates that the predictions from Nagy's (1987) equation are over-exaggerated at least for large eagles. But again, both predictions show how close the prey capture rate by wild black eagles in the present study was to their expected minimum food and energy requirements whether breeding or not. This, no doubt, was due to low hyrax abundance and availability (Chapter 4 & Synthesis). Black eagles might be able to survive on a lower overall prey capture rate than that observed in the present study, but reduced breeding attempts and success would have been expected as a preliminary consequence to any further decline in the prey. At the other extreme, very high rates of prey capture observed by Gargett (1972) probably represent near maximum.

*Factors influencing prey capture rate by black eagles*

Direct and indirect observations on prey capture rate by different black eagle pairs at different times in the study permit investigation of the factors that affect prey capture rate. Certain pairs were consistently good (e.g. GD, KK) or consistently poor (e.g. DH, LH, BR) at catching prey or delivering prey to nests. Using the time-lapse films as sampling units (each representing several days of observations at an eagle's nest), differences in the rate of kills per day could not be demonstrated significantly for the different pairs ($K^2$=8,2; d.o.f.=8; p=0,08). However, when all observations on prey capture rate were pooled for each pair (n=9) and compared with various characteristics of the different pairs by correlation analyses, certain patterns emerged. Most notably, high prey capture rate was associated with pairs which took a large portion of lagomorph prey in their diet as revealed by collections of prey remains (r=0,72; p=0,03). Correlations were stronger with the proportions of scrub hare (r=0,58) and red rock rabbits (r=0,47) in the diet, than with the proportion of Cape hares (r=-0,13). There was also a slight tendency for high prey capture rate to be associated with greater amounts of small grey mongooses in the diet (r=0,57; p=0,11). Greater rates of prey capture might be expected for eagles preying mainly on small red rock rabbits and mongooses, but this reasoning does not explain the observed and stronger association of high prey capture rate with the large scrub hares.

Although the small sample size did not lend itself to statistical testing of associations, these findings were corroborated to some degree when prey capture rate was compared with habitat characteristics of the eagles' territories. There were trends for prey capture rate to be greater in territories which encompassed more middle plateau habitat (r=0,58; p=0,10), more lower escarpment (r=0,54; p=0,14), and less bottom plains habitat (r=-0,63; p=0,07). There was no suggestion of higher prey capture rates by farm birds. Bearing in mind that this analysis is confined to lower escarpment pairs (where time-lapse photography of nests was feasible), peripheral eagle pairs

University of Pretoria etd – Davies, R A G (1994)



which hunted out over the bottom plains (favoured by Cape hares) apparently could not supply as many prey to their nestlings as eagle pairs which hunted over the more rocky, mountainous habitats where scrub hares, red rock rabbits and small grey mongooses were more abundant (Chapters 5 & 9). No associations could be detected between prey capture rate of eagle pairs and the amounts of hyrax in their diets or in their territories. These findings suggest again that the hyrax prey base was well protected within the confines of their rocky habitats, and also probably evenly-distributed between lower escarpment eagle pairs. High levels of food-provisioning by these eagles were evidently more dependent upon a plentiful supply of alternate prey, notably lagomorphs. The increase in red rock rabbit numbers in the park between 1987 and 1989 (Chapter 5) conveniently supplied certain eagle pairs with important additional prey resources.

For the nine pairs with substantial observations on prey capture rate, no associations could be found between prey capture rate and the effort or success of these pairs at breeding. Also there were no detectable associations between prey capture rate and evidence of food stress, such as late breeding or opening of hyrax crania (Chapter 10). This is to be expected because the sample is mostly made up of eagle pairs which, by necessity, were successful breeders (time-lapse photography could not be carried out for non-breeders). A positive correlation between high prey capture rate and successful breeding may have been obtained if there were sufficient data available on prey capture rate for all pairs.

There must be a minimal prey capture rate, below which breeding is not possible. The Lion's Head pair showed a consistently low rate of food provisioning. Their 1989 nestling had to survive intervals of 7-9d between prey deliveries, and their 1987 nestling died from impaction of the crop when it finally received prey after a period of food shortage. The rate of prey deliveries by the Lion's Head pair in 1987 (0,433 prey $d^{-1}$) was the lowest recorded for all monitored nestling periods, and was only slightly higher than the overall prey capture rate observed for non-breeding pairs (0,425 prey $d^{-1}$). The Lion's Head territory contained the most hyrax groups of the four territories mapped (Chapter 6), but they may have been well protected and much of the territory was plains - affording poor flying conditions. The Sloop pair successfully raised a chick in 1989 with an overall prey delivery rate of 0,488 prey $d^{-1}$, but this must be close to the minimum possible provisioning rate for breeding, and these eagles were observed to minimise wastage in 1989 by consuming even the dry hyrax pelts. Consumption of pelts was also observed by Cottrell (1970). Gargett (1990) reported that pelts are sometimes not eaten, so this behaviour (like the opening of hyrax crania - see Chapter 10) may be indicative of the degree of food shortage experienced by the birds.

The absence of a correlation between prey capture rate and breeding success may also be partly due to variation in the hunting and breeding proficiencies of individual eagles or pairs of eagles. The Kortkloof pair achieved a very high level of prey capture in 1989 (0,689 prey $d^{-1}$) but were very poor breeders overall. In this case the female was assumed to be old and laid an infertile egg in 1988. Old eagles may still be able to catch prey, but raptors are known to become less fertile with age (Newton 1979). The success of the Kortkloof pair in 1989 however, may have more to do with the dramatic increase in red rock rabbits in their territory at this time, than with other factors.

The highest rate of food provisioning (0,711 prey $d^{-1}$) was at the Gamka Dam nest in 1988 (this territory had good habitat for red rock rabbits and scrub hares, and the mountainous topography afforded good flying conditions).

University of Pretoria etd – Davies, R A G (1994)



Overall prey capture rate for all monitored pairs was highest (0,625 prey $d^{-1}$) in 1988 and was 27% greater than that in 1987 (0,494 prey $d^{-1}$). In 1989 overall prey capture rate for monitored breeders was 0,562 prey $d^{-1}$. The 1988 nestlings did not have to go longer than 4d without food, whereas certain chicks had to fast for up to 9d in 1989, and for up to 6d in 1987 (Figure 65). These differences in daily prey capture rate between the three years of intensive observation proved to be statistically significant ($X^2$=7,48; p<0,05) when the time-lapse films were used as sampling

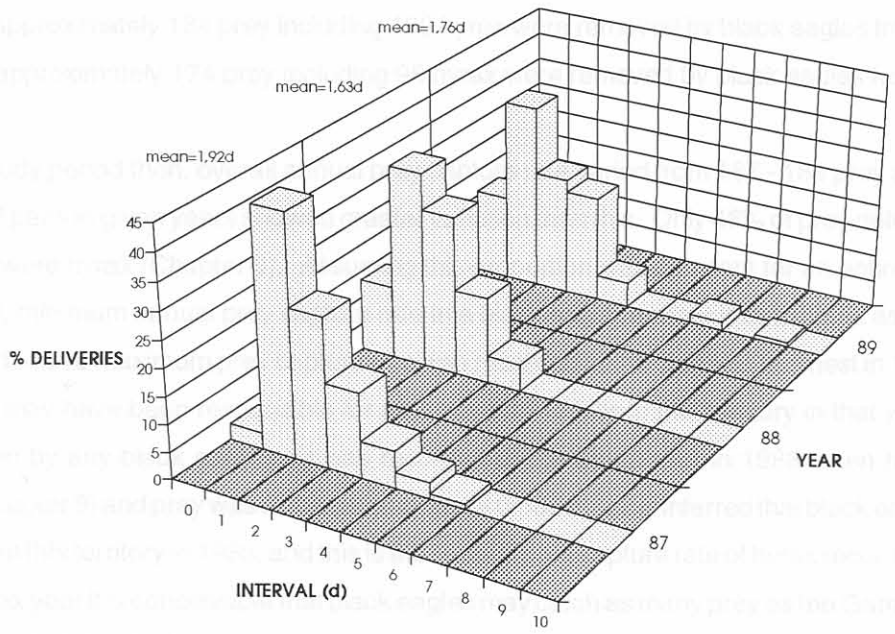



**Figure 65.** Frequency distributions of the intervals between prey deliveries at all nests in the three years monitored.

units for comparison, and can best be explained in terms of long-term changes in prey availability and abundance. Both the December counts at colonies and incidental sightings of hyrax in the veld indicated that the hyrax population declined significantly during 1988 (Figure 40a, page 81). Predation by black eagles was partly responsible for this decline (Chapter 12). Summer rainfall at the end of 1987 and at the end of 1988 was below average for both seasons, leading to impoverished vegetation and possibly increased vulnerability of hyrax to eagle attack. An apparent increase in hyrax availability during 1988 despite their declining abundance is supported by the observation that hyrax comprised the largest portion of prey delivered to eagle nests (as monitored by the time-lapse cameras) in this year (Chapter 9; Fig. 83, p. 198). In 1988 the eagles also took the greatest portion of juveniles amongst their hyrax prey - this is symptomatic of low hyrax:eagle ratio (see Chapter 10), and it probably accounts for increased incidence of opened hyrax crania in 1988 (see Chapter 10, Fig. 98, p. 220). Subsequently prey capture rate declined again in 1989 and hyrax comprised the smallest portion of prey deliveries in this year. This was probably due to significantly reduced hyrax numbers which became less susceptible to attack after rains improved vegetation conditions in 1989. A much lower prey capture rate might have been expected for 1989 had it not been for a seven-fold increase in red rock rabbit numbers between 1987 and 1989 (Fig. 40b, page 81), which was also reflected in the proportion (Chapter 9; Fig. 83, p. 198) and frequency (Fig. 71, p.171) of prey deliveries comprised by this species.

University of Pretoria etd – Davies, R A G (1994)



By combining appropriate data on breeding success, diet and prey deliveries, it is possible to estimate the overall prey capture rate by black eagles in the study area for these three years of intensive study. In 1987 only 33% of pairs raised chicks, average prey capture rate during the breeding season (200d) was 0,494 prey $d^{-1}$ (this can be increased by 4% to compensate for any small prey items that may have been missed by the cameras - see earlier); average prey capture rate by non-breeders can be assumed to be 0,425 prey $d^{-1}$, and by vagrant black eagles 5 prey $yr^{-1}$ (see earlier); and hyrax comprised 73,2% of prey deliveries (Chap. 9). It follows that in 1987 approximately 167 prey including 122 hyrax were removed by black eagles from the average territory. In a similar way it is calculated that in 1988 approximately 184 prey including 136 hyrax were removed by black eagles from the average territory; and in 1989 approximately 174 prey including 98 hyrax were removed by black eagles from the average territory.

During the study period then, overall annual prey capture rate varied from 167 - 184 prey and from 98 - 136 hyrax. But individual pairs in given years showed greater variation than this. Only 46% of prey delivered to the Lion's Head nest in 1989 were hyrax (Chapter 9). Assuming this proportion was constant for an entire year and that the birds did not breed, minimum annual prey capture rate in a black eagle territory is calculated as 160 prey and 73 hyrax. As mentioned above maximum prey capture rate was recorded at the Gamka Dam nest in 1988. It is estimated that black eagles may have been responsible for as many as 217 kills in this territory in that year. But the highest toll of hyrax taken by any black eagle pair was recorded at the Sloop nest in 1988 when hyrax comprised 83% of deliveries (Chapter 9) and prey was delivered at a rate of 0,586 $d^{-1}$. It is inferred that black eagles may have removed 159 hyrax from this territory in 1988, and this is the highest prey capture rate of hyrax recorded for the present study. In a good hyrax year it is conceivable that black eagles may catch as many prey as the Gamka Dam pair did in 1988, and that 83% of all these might be hyrax. In this scenario black eagles might be expected to remove as many as 181 hyrax from a territory in one year. This is the upper limit to prey capture rate that is indicated by this study. However it is still only half an early estimate of hyrax predation by single black eagle pairs in the Matobo Hills (Gargett 1972). Gargett later (1990) estimated the annual toll to be 321 hyrax / territory / year. As mentioned earlier, Gargett's observations were conducted when hyrax may have been highly available, and mean prey mass may possibly have been lower in her study. Gargett's estimate is based on one pair in one season, so it should not be extrapolated to indicate an overall prey capture rate for the Matobo. Even if the eagle pairs in the present study maintained maximum (breeding) prey capture rate throughout the year and ate solely hyrax, total annual toll would be about 270 hyrax per territory. It is considered highly unlikely that karoo black eagle pairs would ever kill more than 350 hyrax per annum. This is more than double the overall prey capture rate recorded in the present study, so wastage at this level of predation would be excessive.

Variation in prey capture rate within the year, in and out of the nesting season, has already been treated. Within the nestling period some variation in prey capture rate might be expected, for instance with the food requirements of the chick (see earlier), or with nest-attendancy by the adults. The proportion of time that any adults were attending their chicks was assessed for four nestling periods using the time-lapse films. This is shown in Figure 66 in relation to chick age. Nest-attendancy was apparently climate-related. A south-facing nest (KK) which was not exposed to the sun experienced lowest nest attendance by adult birds; whereas a north-facing nest (SL) experienced prolonged nest-attendancy by the adult birds into the second month of the nestling period, presumably while they afforded shade to their nestling from the hot sun. The overall pattern showed that adults were very attentive (about

University of Pretoria etd – Davies, R A G (1994)



80% time) for the first three weeks, but thereafter nest attendance declined to about 20% of the time by the sixth week and to only 10% of the time for the last few weeks of the nestling period. This suggests that endothermy of black eagle chicks develops from about 20d old which is a week later than in golden eagle chicks (Collopy 1980). Gargett (1990) recorded nest attendances of 83% in the first month of the nestling period, about 35% in the second month and 19% in the last month. Slightly higher nest attendancy by Matobo eagles may be due to a hotter environment and/or reduced food stress. The need for high nest attendancy by at least one adult in the first few weeks of the nestling period means that tandem-hunting by nesting adults can only re-commence when the chick is 4-5w old. Hunting success by tandem-hunting adults appeared to be greater than by adults hunting solo (Chapter 6). One would expect prey deliveries to increase when the chick reaches 4-5w old, which is also the period of maximum food consumption by the chick. Weekly prey delivery rate was assessed from the time-lapse films for 10 more or less complete nestling periods. Prey delivery rate to these nestlings was highly erratic even for the same pairs in different years or for different pairs in the same years (Figure 67 - overleaf). Prey delivery was erratic for both hyrax and other prey items but a heavy reliance on other prey was evident in 1989 for KK and LH (Figure 67). Overall weekly prey delivery rate was fairly constant throughout the nestling period when data for all 10 nestlings were combined, and showed no significant relationship to either nest attendancy or food requirements of the chick (Figure 68 - below). This implies that the male must make a greater effort to compensate for the poorer success of solo-hunting during

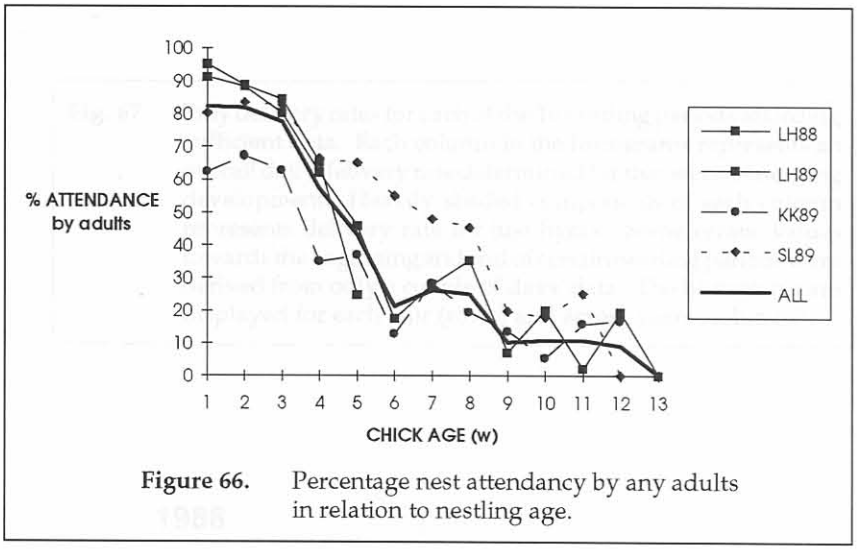



**Figure 66.** Percentage nest attendancy by any adults in relation to nestling age.

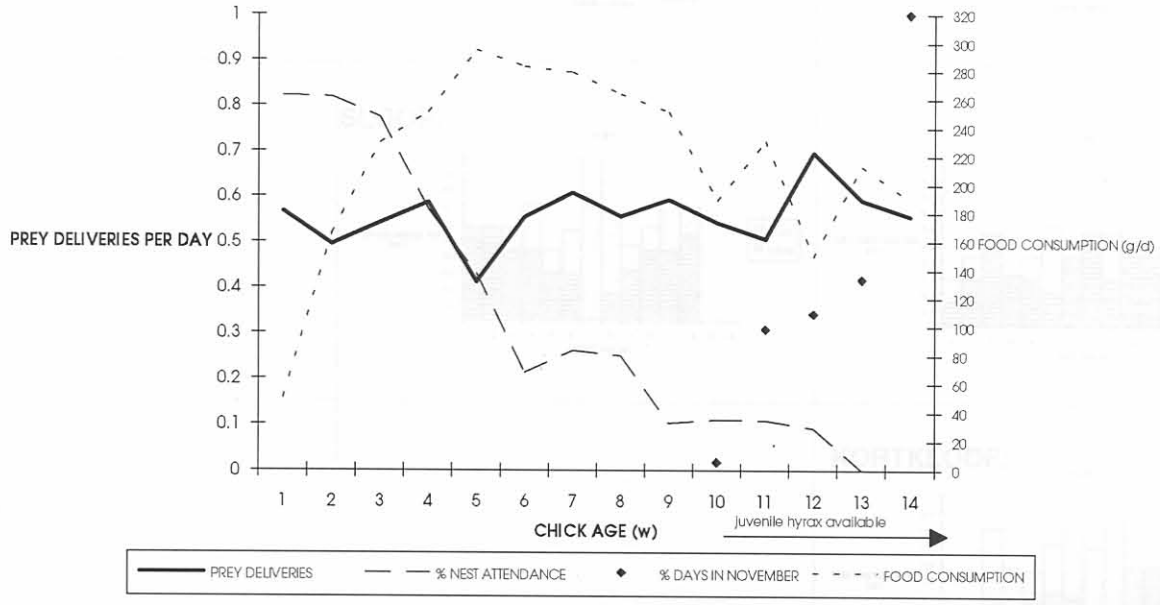


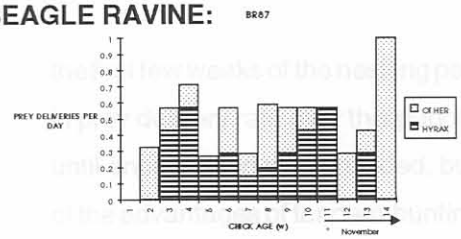

**Figure 68.** Change in overall prey delivery rate (to all nests) with nestling age, in relation to nest attendancy by adults and food need of the nestlings. The proportion of days in November is also shown for the end of the nestling periods when juvenile hyrax become available.

University of Pretoria etd – Davies, R A G (1994)

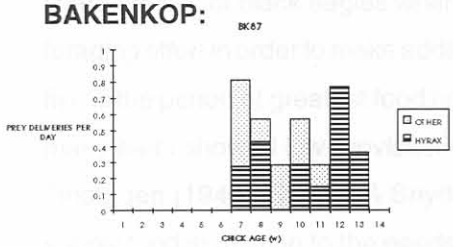


**1987** | **1988** | **1989**

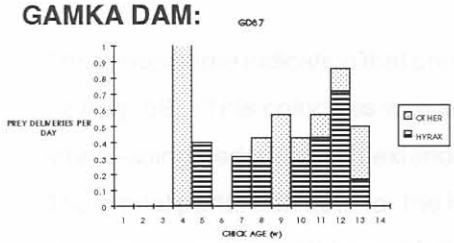
**BEAGLE RAVINE:**

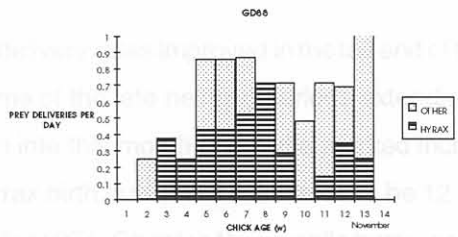



**BAKENKOP:**

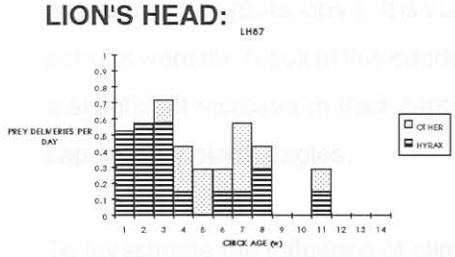


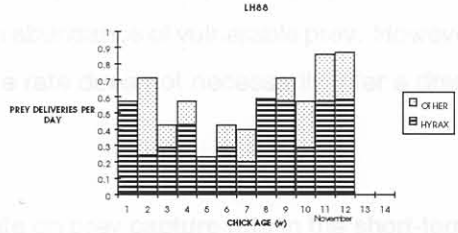

**GAMKA DAM:**

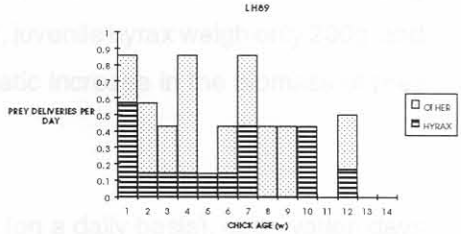


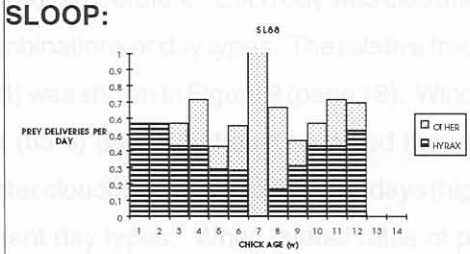

**LION'S HEAD:**

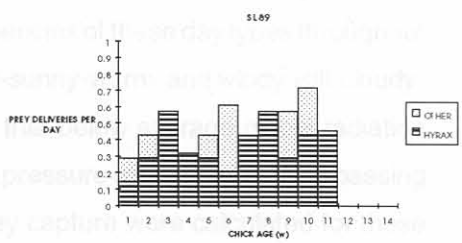



**SLOOP:**




**KORTKLOOF:**

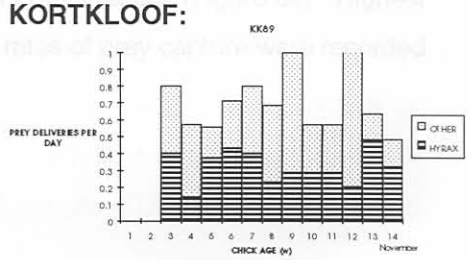



Fig. 67. Prey delivery rates for each of the 10 nestling periods affording sufficient data. Each column in the histograms represents an overall daily delivery rate determined for that week of nestling development. Heavily shaded components of each column represents delivery rate for just hyrax. Some erratic values towards the beginning and end of certain nestling periods were derived from only a couple of days' data. The histograms are displayed for each pair (rows) and across years (columns).

University of Pretoria etd – Davies, R A G (1994)



the first few weeks of the nestling period. Only for one nestling period (GD88) out of ten was there a distinct reduction in prey delivery rate over this period (Figure 67). It appears that hunting effort by the eagles might have increased until enough food was provided, but that when sufficient food was obtained the birds did not make additional use of the advantages of tandem-hunting to supply a surplus of prey to the nest. This would comply with the observation in Chapter 6 that black eagle foraging behaviour is highly 'state-dependent'. Prey surpluses on nests may only be characteristic of black eagles where prey is superabundant and when the eagles do not have to make much extra foraging effort in order to make additional kills, as perhaps may have been the case in the Matobo Hills in 1970. Week five is the period of greatest food need on the nest and occurs at a time when the female can join in the hunting, yet many pairs showed low provisioning rates for this period (Figures 67 & 68). These findings corroborate those of Tinbergen (1940), Snyder & Snyder (1973), Newton (1978) and Collopy (1980), that raptors do not necessarily supply food in relation to the needs of their broods, and that provisioning is probably most influenced by prevailing conditions of foraging success.

There was some indication that prey delivery rates improved in the tail end of the nestling period, particularly in week 12 (Fig. 68). This coincides with some of the late nestling periods extending into November. In fact, three of the four nestling periods which extended into this month showed a marked increase in prey capture rate (Figure 67). The modal parturition date for the hyrax birth pulse was calculated to be 12 November, and probably at least 80% of juveniles are born in this month (Millar 1971; Chapter 4). Juvenile hyrax were usually first seen early in November, but one was recorded in late October. Just after birth, hyrax are very naive towards predators and are easily caught by black eagles (pers. obs.). It is very likely then that improved prey delivery rates recorded at the end of late nestling periods were the result of this sudden abundance of vulnerable prey. However, juvenile hyrax weigh only 200g, and a significant increase in their capture rate does not necessarily infer a dramatic increase in the biomass of prey captured by black eagles.

To investigate the influence of climate on prey capture rate in the short-term (on a daily basis), observation days were classified in terms of the three principal climatic parameters that were considered potential influences on eagles or their prey: wind speed, sunshine and temperature. Each day was classified as above or below average in terms of these parameters to give eight combinations or day types. The relative frequencies of these day types throughout the entire period of field study (1265d) was shown in Figure 8 (page 18). Windy-sunny-warm, and windy/still-cloudy-cool conditions accounted for most (65%) days. It should be noted though that below average global radiation (sunshine) might not necessarily confer cloudiness. Still-sunny-cool days (high pressure conditions after the passing of a cold front) were the least frequent day types. When overall rates of prey capture were calculated for these different day types (from both the time-lapse films and direct observations), a statistically significant association was demonstrated between prey capture rate (all prey types) and certain weather combinations (Figure 69). Highest rates of prey capture were recorded on windy-sunny-cool days, while lowest rates of prey capture were recorded on still-sunny-cool days.

University of Pretoria etd – Davies, R A G (1994)



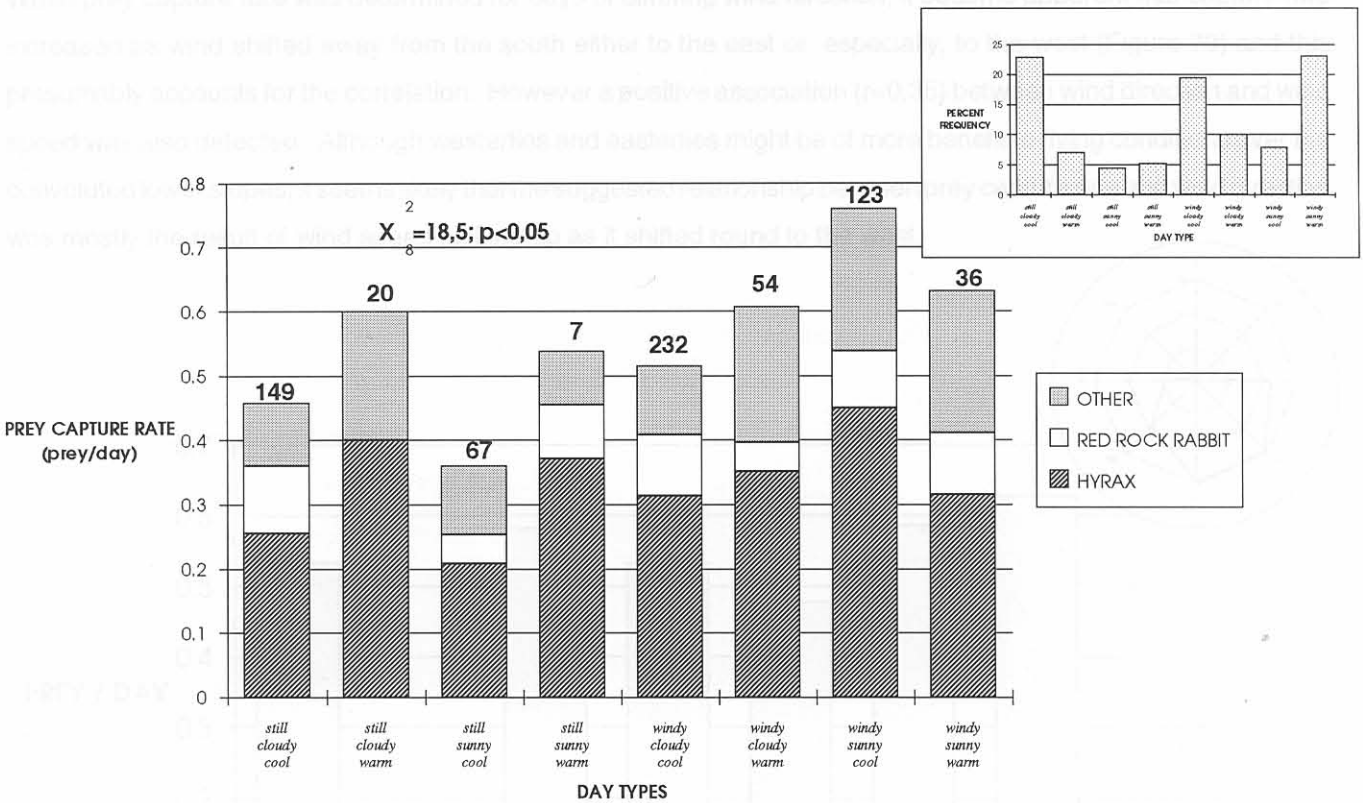



**Figure 69.** Overall delivery rates of hyrax, red rock rabbits and other prey to black eagle nests on different types of day (days were classified as above or below average for three important climatic variables). The frequency of these day types during monitoring by time-lapse photography is given at the top of each column. The frequency distribution of day types throughout the study period (1265d) is shown as an insert of Fig. 8 from page 18.

---

Capture of hyrax specifically appeared to be largely responsible for this trend (Fig. 69), and the particular weather combinations suggested that wind was the key factor. Indeed, prey delivery rate to nests on windy days (0,61 prey $d^{-1}$) was found to be nearly 40% greater than prey delivery rate on still days (0,44 prey $d^{-1}$), and this difference proved to be statistically highly significant ($X^2$=10,2; p<0,01). Wind is known to enhance black eagle flying and foraging behaviour (Chapter 6). By contrast, the efficiency of the early warning system employed by hyrax on group foraging bouts would be severely impaired by windy conditions because individuals travelling down to riparian thickets may be unable to hear the alarm calls of the sentinels. It is relevant to note that hyrax did not embark on group foraging bouts down to riparian thickets on very windy days (Chapter 4). This behaviour was most prevalent on still-sunny-cool days after cold fronts - when prey capture rate by eagles was lowest (Fig. 69).

When correlation analyses were employed on a daily database to investigate possible associations between prey delivery rate to nests and a variety of climatic factors, the same influence of wind speed was detected (r=0,14; p=0,02), as well as a significant positive association with wind direction measured as degrees from true north (r=0,14; p=0,02), although the latter relationship was lost for some reason when direct observations on prey capture rate were

University of Pretoria etd – Davies, R A G (1994)



included in the sample. Wind in Beaufort West emanates mainly from the south and south-east (Fig. 7, page 18). When prey capture rate was determined for days of differing wind direction, it became apparent that capture rate increased as wind shifted away from the south either to the east or, especially, to the west (Figure 70) and this presumably accounts for the correlation. However a positive association (r=0,35) between wind direction and wind speed was also detected. Although westerlies and easterlies might be of more benefit to flying conditions over the convoluted lower slopes, it seems likely that the suggested relationship between prey capture rate and wind direction was mostly the result of wind speed picking up as it shifted round to the west.

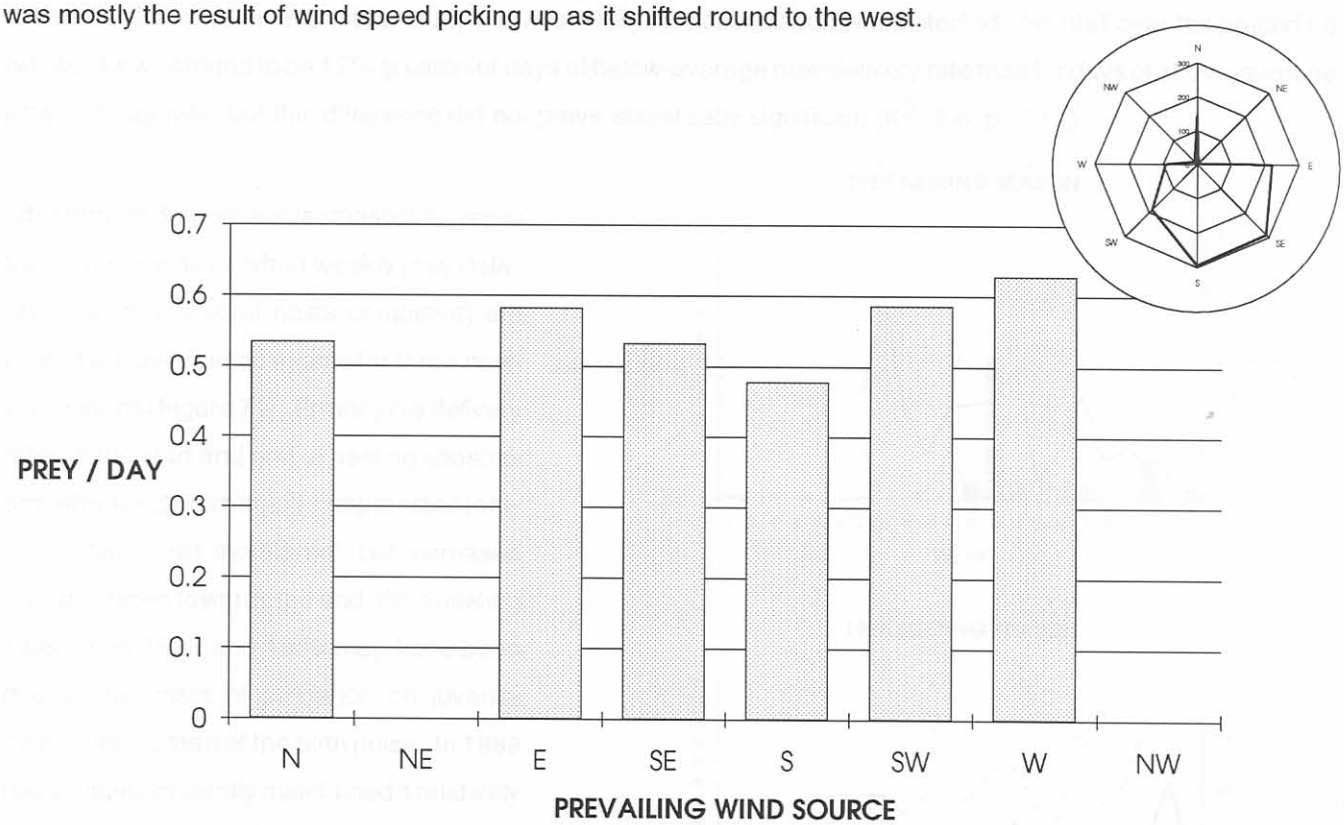



**Figure 70.** Prey delivery rates to black eagle nests for days of different wind directions. Frequencies of different wind directions over the study period (1265d) are shown as an insert of Fig. 7 from page 18.

No other associations between total prey or hyrax capture rates and climatic factors were detected by this correlation analysis, but there were statistically significant indications that fewer red rock rabbits were captured on longer (summer) days (r=-0,12; p<0,05) and on very humid days (r=-0,12; p<0,05). It seems unlikely that red rock rabbits were less abundant on these days. Perhaps the rabbits occupy more vulnerable 'forms' or are more active on short winter days. Reduced capture rates of red rock rabbits on long summer days was countered by increased capture rates of other 'non-hyrax' prey types (r=0,11; p<0,05). Capture rate for the latter (which includes unidentified prey) was also significantly greater on sunny days (r=0,20; p<0,01). It is not clear why this category should be more vulnerable to eagle attack on days of high global radiation but these relationships are not necessarily consequential.

Daily atmospheric pressure and rainfall were not related to daily prey capture rate in any obvious detectable way. But rainfall can be expected to have some negative influence on the capture of hyrax by eagles either directly, or indirectly mediated through the vegetation. Heavy rains are known to keep hyrax in their shelters for up to three days

University of Pretoria etd – Davies, R A G (1994)



(Coe 1962; pers. obs.). Within days or weeks, good rains can replenish over-grazed vegetation resources in the immediate vicinities of hyrax colonies. Certain plants are known to respond within a day to very small rainfall events (5mm) in semi-arid regions (Sala & Lauenroth 1982). After significant rains, hyrax should be able to fulfill their forage requirements within a safer distance of their rocky shelters, and perhaps within a shorter time period. To test the hypothesis that hyrax vulnerability declined after rains, daily prey capture rates were correlated with a measure which summed rainfall for the preceding 40d for each observation day. This measure was found to be a useful indication of karoo veld condition in another study (Davies 1985). No association was detected. Rainfall over the preceding two weeks was found to be 17% greater for days of below-average prey delivery rate than for days of above-average prey delivery rate, but this difference did not prove statistically significant ($K^2$=2,6; p=0,11).

Although not demonstrable statistically, some trends are apparent when weekly prey delivery rates (for several nests combined) are plotted against rainfall events for three nesting seasons (Figure 71). Erratic prey delivery rates at the start and end of nesting seasons probably result from small sample sizes (only one or two nests monitored), but increased prey deliveries towards the end of the nesting seasons in 1988 and 1989 may have been due to the onset of predation on juvenile hyrax with the start of the birth pulse. In 1989 black eagles evidently maintained a relatively constant prey delivery rate while shifting emphasis from red rock rabbits at the start of the season to hyrax at the end of the season. The matter of 'switching' from one prey to another is treated in Chapter 9. There was some indication of a gradual increase in hyrax delivery rate during extended dry spells in 1988 and 1989. A decline in hyrax delivery rate one to two weeks after rainfall events was not very clear in 1989, but was very apparent in 1987 and 1988. Delivery rates for all prey are influenced by these patterns in hyrax deliveries. Delivery rate of red rock rabbits however, appeared to be largely independent of rainfall events. These patterns are suggestive that hyrax vulnerability does decline somewhat after rainfall (in agreement

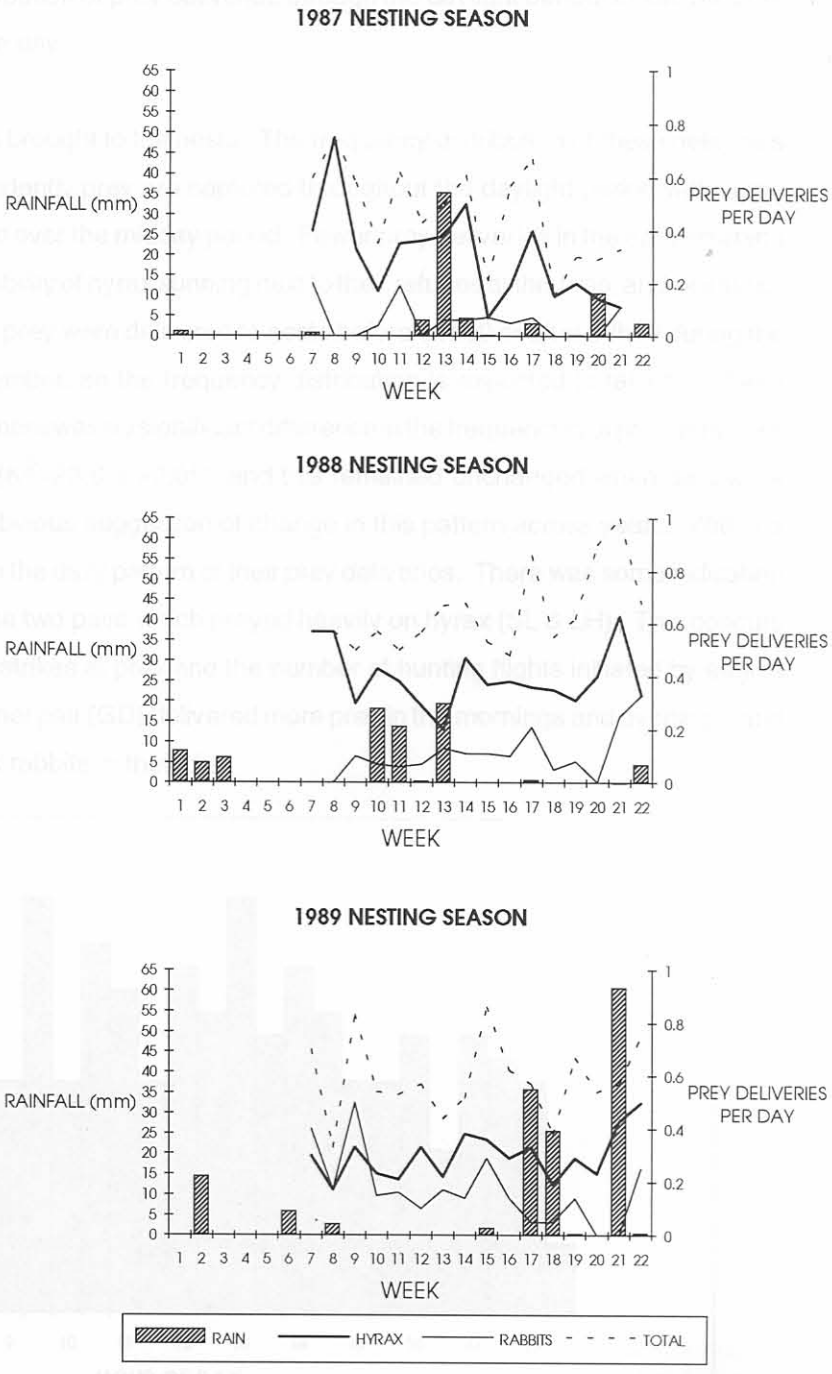



**Figure 71.** Delivery rates of hyrax, red rock rabbits and all prey to black eagle nests for the three nesting seasons monitored, in relation to the timing and magnitude of any rainfall events. (values were calculated by week).

University of Pretoria etd – Davies, R A G (1994)



with indications from direct observations of hyrax movements - see Chapter 4, and relationships between eagle breeding success and rainfall - see Chapter 6), but the magnitude of the decline and its timing after the rainfall event probably vary with many factors, especially the size of the event, the degree of drought-stress and the hyrax population pressure.

The time-lapse films could also be analysed for diurnal variation in prey capture rate. Timing of prey deliveries or other events on nests could be determined within an accuracy of 10min (see earlier) from the time-lapse films. Although the timing of prey deliveries to nests does not exactly represent the timing of prey capture, direct observations indicated that prey was usually delivered immediately to nests after capture and not later than 40min after capture if the captor fed first. So the distribution of prey deliveries through the daylight period should be a fair indication of the distribution of kills through the day.

Timing of delivery was determined for 293 kills brought to the nests. The frequency distribution of these deliveries for 30min intervals is shown in Figure 72. Evidently prey are captured throughout the daylight period with some indication that more are captured and delivered over the midday period. Fewer prey deliveries in the early morning (06h00 - 08h00) may be due to reduced vulnerability of hyrax sunning next to their refuges at this time, and/or inferior flying conditions for the eagles at this time. No prey were delivered to nests before 06h00 or after 18h29 during the shorter, late winter days in August and September, so the frequency distribution is expected to tail off at these extremes. With these time intervals excluded, there was no significant difference in the frequencies of prey deliveries for different time periods throughout the day ($K^2$=23,6; p>0,05), and this remained unchanged when data were analysed on an hourly basis. There was no obvious suggestion of change in this pattern across years. Within a year, different pairs did show a wide variation in the daily pattern of their prey deliveries. There was some indication of a 3 - 4 hourly rhythm in prey deliveries for the two pairs which preyed heavily on hyrax (SL & LH). This concurs with a similar activity rhythm in the number of strikes at prey and the number of hunting flights initiated by eagles indicated in Chapter 6 (Fig. 47, page 95). Another pair (GD) delivered more prey in the mornings and evenings, and this may relate to a greater portion of red rock rabbits in their diet.

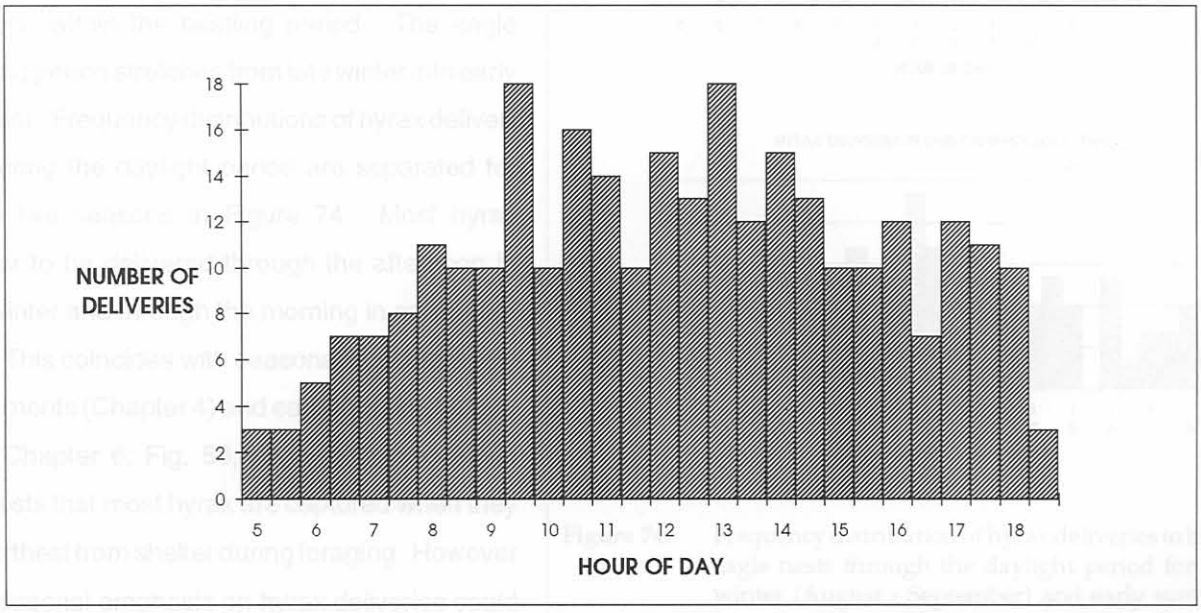



**Figure 72.** Frequency distribution of all prey deliveries (n=293) to black eagle nests throughout the daylight period.

University of Pretoria etd – Davies, R A G (1994)



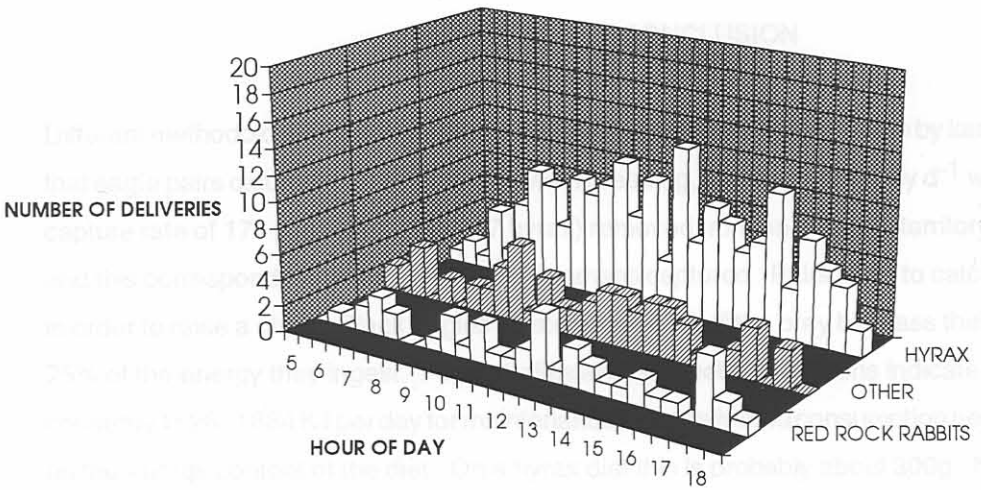



**Fig. 73.** Frequency distribution of hyrax, red rock rabbit and other prey deliveries to black eagle nests throughout the daylight period.

Frequency distributions of the timing of deliveries are shown for different prey types in Figure 73. Red rock rabbits were delivered to nests throughout the day indicating that this nocturnal and cryptic species might be vulnerable to eagle attack at almost any time of the day. Perhaps many of these rabbits are detected and captured when they move resting sites in response to microclimate change. But there was no obvious indication of a clumping of rabbit deliveries around the midday period. Early morning and late evening deliveries of red rock rabbits may represent animals captured while they are actively foraging, indicating auroral and crepuscular habits. Other prey (including a large unidentified element) were also delivered in the mornings and evenings with no obvious suggestion of a midday peak, unlike the hyrax deliveries. The pattern of hyrax deliveries (which tails off in the mornings and evenings) is evidently largely responsible for the overall pattern. The absence of any obvious 3-4h rhythm amongst these deliveries may be due to the confounding influences of variation between pairs and between different seasons within the nestling period. The eagle nestling period stretches from late winter into early summer. Frequency distributions of hyrax deliveries during the daylight period are separated for these two seasons in Figure 74. Most hyrax appear to be delivered through the afternoon in late winter and through the morning in early summer. This coincides with seasonal hyrax foraging movements (Chapter 4) and eagle hunting behaviour (Chapter 6: Fig. 58, page 122), and again suggests that most hyrax are captured when they are furthest from shelter during foraging. However the seasonal emphasis on hyrax deliveries could not be demonstrated statistically ($K^2$=3,2; p>0,10).

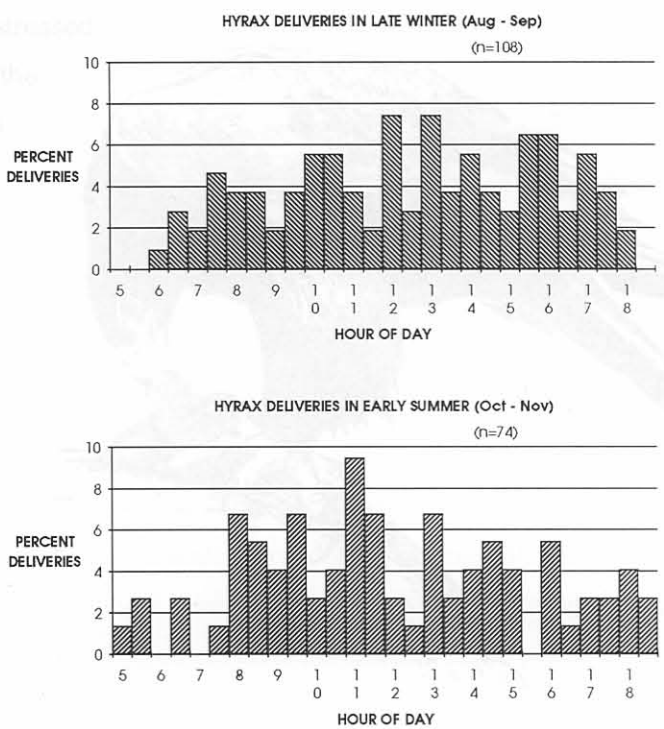



**Figure 74.** Frequency distribution of hyrax deliveries to black eagle nests through the daylight period for late winter (August - September) and early summer (October - November).

University of Pretoria etd – Davies, R A G (1994)


# CONCLUSION

Different methodologies employed in the determination of prey capture rate by karoo black eagles largely concurred that eagle pairs catch about 0,6 prey $d^{-1}$ when breeding, and about 0,4 prey $d^{-1}$ when not breeding. An overall prey capture rate of 174 prey (including 117 hyrax) removed from an average territory is indicated for an average year, and this corresponds to about 446kg prey biomass captured. Pairs need to catch an additional prey item every 6d in order to raise a chick. Black eagles waste about 40% of the prey biomass they capture and probably assimilate 75% of the energy they ingest. Food studies and energetic predictions indicate that a 3,8kg black eagle needs to consume 1526 - 1684 KJ per day for maintenance. The daily food consumption necessary to achieve this will depend on the energy content of the diet. On a hyrax diet this is probably about 300g. Nestling black eagles may be able to get by on less than this overall, whereas active wild adults may need up to 25% more. The indications from this study are that prey capture rate may vary from about 160 prey and 70 hyrax per territory per year up to 220 prey and 180 hyrax per territory per year. Other studies indicate an absolute upper limit of 350 hyrax captured per pair in years of optimal prey availability. Estimates of prey capture rate in this study were generally lower than those recorded for large eagles elsewhere but because of large prey size, the indications on biomass captured were not so different. Predictions of minimum predation requirements suggest that the eagles in the present study were operating very close to this. Better provisioning by eagle pairs with a good supply of alternate prey (lagomorphs) indicates that hyrax were not very available since their recent decline. Prey capture rate was found to vary more with changes in prey availability than with changes in eagle food requirements or with changes in their potential hunting abilities. Prey availability can mostly be related to climate. Good rains probably improve prey abundance in the long-term but appear to lead to temporary reductions in prey vulnerability through vegetation effects. Hyrax were most heavily preyed upon when most drought-stressed.

Prey capture rate is also influenced by behaviour of the prey and predator. More prey were caught on days when wind assisted eagle hunting behaviour, and possibly at times of the day when foraging behaviour by the prey may have rendered them more vulnerable to attack.



University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 9*

# *BLACK EAGLE FEEDING HABITS - 2. COMPOSITION OF PREY SPECIES IN THE DIET*

## INTRODUCTION

The diet of black eagles has been extensively researched by the collection of prey remains from under nesting cliffs in five major regions of southern Africa. Earlier work in two of these regions indicated that black eagles are highly specialized, almost obligate predators on rock hyrax (genus *Procavia* and *Heterohyrax*): this prey taxon comprised 98,2% of 1892 prey items collected beneath nest cliffs in the Matobo Hills, Zimbabwe (Gargett 1977); and 92,6% of 176 items collected in the Transvaal, South Africa (Tarboton & Allan 1984). These observations that rock hyrax make up over 90% of black eagle prey have been widely cited in the literature (e.g. Cramp & Simmons 1980; Brown, Urban & Newman 1982; Steyn 1982; Maclean 1985), but detailed analyses of recent extensive collections of prey remains from three major biomes in the Cape Province, South Africa by Boshoff *et al.* (1991), indicate that black eagles can be versatile predators: non-hyrax prey comprised 11,3% of 3623 items collected in the Karoo; 38,2% of 1370 items collected in eastern Cape grasslands; and 52,3% of 755 items collected in the Fynbos. Other prey taxa represented in these regions were lagomorphs (4,8 - 8,6% diet); small carnivores (1,8 - 5,2%); juvenile domestic bovids (2,3 - 7,3%); juvenile wild bovids (3,7 - 5,0%); birds (0,6 - 10,2%); reptiles (0,9 - 9,3%); rodents (0,1 - 10,5%); and primates (0 - 2,0%).

To date, these analyses of prey 'left-overs' represent the only extensive investigations of black eagle diet. Direct observations of the eagles with prey are very scant, but apart from one study (Jenkins 1984), most indicate a more catholic diet (e.g. Rowe 1947; Branfield 1990; Boshoff *et al.* 1991), with incidental observations of peculiar hunting behaviour such as dropping tortoises to the ground (Steyn 1984; Fraser 1985). Evidently black eagles can hunt opportunistically, and there is accumulating evidence that they may be able to successfully make use of alternate prey at sites where rock hyrax are scarce. This raises speculation that black eagles might not be rock hyrax specialists, but rather catch the most available prey species living in African mountainous regions.

The high representation of rock hyrax in collections of prey remains might also result, in part, from various biases inherent in using prey remains to determine diet (Boshoff & Palmer 1980; Brown 1988c; Brown & Plug 1990; Boshoff *et al.* 1990). The sturdy skulls of rock hyrax are likely to be more noticeable, more resistant to weathering and more easily identified than prey remains from lagomorphs, rodents, small carnivores and birds. Collopy (1983b) appraised collections of prey remains as a means of investigating golden eagle *Aquila chrysaetos* feeding habits, against direct observations of prey on the nests. He found no significant differences between species composition of diet as indicated by the two methods, but the prey remains in this case were collected directly off the nests of the eagles 43-45 times each nesting season. It is likely that most of the black eagle work referred to above was carried out by collecting remains from beneath the eyries on one or two visits.

University of Pretoria etd – Davies, R A G (1994)



It is clear that a comprehensive study of black eagle feeding habits involving extensive use of alternate methods would reveal any biases in the collection of prey remains, and would also provide insight to the degree of specialism of the black eagle as a predator. The latter requires detailed knowledge of the prey base which is provided in the present study (Chapters 4 & 5). Specialist predators, by pursuing their prey at low densities, may have a destabilising affect upon prey populations (e.g. Pearson 1966, 1971; Fitzgerald 1977; Henttonen 1985; Korpimäki, Norrdahl & Rinta-Jaskari 1991), so this may have an important bearing on the predator-prey system under investigation.

The amount of rock hyrax in the diet of the eagles coupled with the rate at which prey are captured (previous chapter), are important parameters which need to be accurately measured for the interpretation of the demographic influence of black eagle predation on rock hyrax. Dietary selection of the different components of rock hyrax populations is also very important in this regard and is treated in the next chapter. The dominance of rock hyrax among black eagle prey and the ratio of predator to prey biomass can also give an indication of the likelihood of co-evolution occurring in this system (Allen 1976).

By investigating variation in black eagle diet over time and at different localities, it may be possible to identify the ecological factors that affect dietary selection of prey species and age classes. Analyses of black eagle diet at farm sites can provide a measure of the beneficial versus the harmful effects of this predator with regard to small stock husbandry (this important aspect of black eagle predation on karoo farms is treated more fully in Chapter 11). Temporal and geographical variation in predator diet can also be a useful indicator of processes affecting ecological communities (Andrews 1990; Avery 1992).

Prey remains collected during 1986 and 1987 within the study area (n=2250 items) made up part of the karoo sample analysed by Boshoff *et al.* (1991). This chapter presents analyses of the full sample of black eagle prey remains collected in the study area to date (including a further 1573 items collected between 1988 and 1990). These collections are now housed at the South African Museum in Cape Town along with other material reviewed by Boshoff *et al.* (1991). The full collection at the museum now totals over 6000 items thought to have been fed upon by black eagles in the Cape, and so provides a substantial database which is extensively referred to in this and the following chapter.

Analyses of the KRNP prey remains collections are supplemented in this chapter with data on black eagle feeding habits derived from three alternate methods: time-lapse photography at nests; direct observations of prey leftovers on nests; and direct observations of hunting and feeding behaviour of the eagles. A detailed appraisal of the four methods is necessary for data interpretation. Overall black eagle diet is determined from an interpolation between these various methods and discussed in relation to prey availability to draw conclusions on the degree of specialisation shown by black eagles. The main factors influencing variation of diet in time and space are also considered. On account of the multiple topics treated in this chapter, the results and discussion sections have been merged.

University of Pretoria etd – Davies, R A G (1994)



# METHODS

*The collection of prey remains from eagle nest cliffs*

At the end of each black eagle nesting season (December/January) during the study period, an intensive search was made beneath the nest and roost cliffs of as many black eagle pairs as possible to look for the remains of any prey items. With experience, it became possible to predict exactly where to search for individual pairs, but some feeding sites were not discovered until the second or third collections. Despite intensive searching of all areas there was wide variation in the number of prey items per collection. Factors influencing this variation are discussed later. Attempts were made to remove all prey remains from the sites at each collection, but undoubtedly some remains were overlooked, so the season of collection does not necessarily reflect the year of capture (particularly for the first collections).

Screes and accessible krantzes (small cliffs) in the vicinity of nests yielded most material. Regular feeding spots, popularly known as 'butcher blocks' (Cowden 1969; Gargett 1990), were discovered for certain pairs. First collections at such sites could yield up to 300 prey items. Low compact growths of the shrub *Grewia robusta* were favoured, and the tops of these shrubs often appeared pruned to form a flat solid platform of twigs and leaves into which remains of past meals had become interwoven. These platforms presumably provided the eagles with a good grip while they dismembered their prey, free from dust and soil. Many remains were found under surrounding shrubs where they had become ensnared by the vegetation on the steep slope. At some sites there was evidence that the prey remains had been scavenged by small carnivores (possibly mongooses), and cached by these animals under boulders. Skeletal material in such micro-climates and buried under top soil were less decomposed than material exposed on the slopes. Besides the skeletal material, skin, feathers and regurgitated pellets were also collected. The age (since death) of all skeletal material collected was ranked as fresh, medium or old in accordance with the degree of decomposition (allowances were made for micro-climate - see detailed methodology in Chapter 10).

For each item collected, a subjective assessment had to be made as to whether it actually represented prey of the eagles. The possibility that other predators were using the same feeding stations as the eagles cannot be ruled out, but for the sake of consistency, all material found under obvious 'butcher blocks' was collected as eagle prey, even unlikely items such as Alpine swift *Apus melba*. Rock hyrax skulls collected at butcher blocks were often opened with characteristic triangular sections removed from the occipital region of the cranium, presumably to access the brain as observed by Gargett (1990). Similar signs were used to identify other eagle prey, but further from feeding and nesting sites the possibility that material represented non-violent mortality, or the work of another predator was considered. Rock hyrax carcasses discovered in thick vegetation or under boulders, the skin of which had been folded inside-out, were considered to be caracal prey (after P. Benadie & L.C. Moolman pers. comm.). Some rodent material was excluded as more likely killed by rock kestrels; while some bird material was thought to have been killed and fed on by resident peregrine falcons. Skeletal material of black eagles probably resulted from non-predatory mortality in the vicinity of the nest cliffs - complete skeletons were usually found. Cape vultures have been known to be killed by black eagles (e.g. Bowen 1970; Mundy *et al.* 1986), but bones of immature vultures collected beneath some very tall cliffs in the KRNP were thought more likely to indicate an extinct colony.

University of Pretoria etd – Davies, R A G (1994)



To decide whether skeletal material of very large animals found under nest cliffs represented prey that was killed or scavenged by the eagles, it was necessary to know likely upper limits on the size of animals that might be overpowered and carried by the eagles - these figures were derived from the literature. Golden eagles have been known to get airborne with dall sheep lambs *Ovis dalli dalli* weighing 10 - 12kg, but only when descending from windy slopes (Nette, Burles & Hoefs 1984). From observation of a captive bird, it seems unlikely that black eagles would be able to convey any prey larger than about six kilograms to their nests or feeding sites unless it was dismembered first. The largest prey delivered to black eagle nests being monitored by time-lapse cameras (previous chapter) was a klipspringer lamb, estimated to weigh approximately 3,6kg. Records of maximum prey size for large eagles are summarised in Table 26. Eagles are evidently capable of killing some enormous prey, but most of the very large

TABLE 26
MAXIMUM SIZE RECORDS FOR PREY KILLED BY EAGLES

| Source | Eagle | Prey | Size |
|---|---|---|---|
| Lehti (1947) | golden | pronghorn | 36,3kg |
| Letley (1962) | black | grey rhebok | 9 - 14kg |
| Cooper (1969) | golden | red deer | 20,5kg |
| Bruns (1970) | golden | pronghorn | 31,7kg |
| Skogland (1974) | golden | reindeer | 25kg |
| Svendsen (1980) | golden | domestic sheep | 25kg |
| Steyn (1982) | crowned | bushbuck | 30kg |
| O'Gara et al. (1983) | golden | domestic sheep | 20 - 25kg |
| Bergo (1987) | golden | red deer | 30 - 50kg |

items killed by golden eagles were weakened by harsh winter conditions. It is possible that some of the largest prey recorded for golden eagles may have been driven over cliffs (Bergo 1987). Brown *et al.* (1982) contend that black eagles can kill prey up to 10kg in weight. I chose 18kg as the cut off point for the maximum prey size that could be killed by black eagles, and assumed that anything above this would have had to be scavenged. This is about half the size of a full-grown domestic sheep. Assignment of estimated mass to prey items is discussed later. Intact skeletons of adult grey rhebok and domestic sheep or goats were excluded from the sample on the presumption that they died on the cliffs and were not dismembered by the eagles.

University of Pretoria etd – Davies, R A G (1994)



After these exclusions it is still not possible to be certain that the remaining material was fed on by the eagles. White-necked ravens may well have been partly responsible for an unusually large collection of greater padloper tortoise *Homopus femoralis* remains found beneath a black eagle nest cliff on the upper escarpment. It is also not possible to be sure about the separation of predated versus scavenged material, and it seems likely that a great many juvenile large bovids and adult small bovids would have been scavenged rather than killed and dismembered as assumed here.

Each collection was separated into hyrax and non-hyrax remains and then analysed separately. With a bit of practice, rock hyrax skeletal material is very readily identifiable from its sturdy and curvaceous nature. Limb and pelvic bones were separated for left and right and counted along with sacra, but highest counts of individuals were nearly always obtained from maxillae. These had often broken into left and right maxillae in very decomposed specimens. Only for small juveniles did I sometimes obtain a higher individual count using left and right mandibles. Vertebrae and ribs were not quantified. The high representation of rock hyrax by cranial and dental material is fortunate because it facilitated separation of nearly all individuals by sex and age class. The allocation of rock hyrax prey into separate components of the population on the basis of dental characteristics and the calculation of mass for rock hyrax prey is outlined in full and treated separately in Chapter 10.

Under the supervision of G. Avery, non-hyrax prey remains were identified by comparison with osteological material housed at the Archaeology Department of the South African Museum in Cape Town. Limb and pelvic bones were separated for left and right and counted along with sacra, sterna (in the case of birds), scutes (in the case of tortoises) and skull material to give a minimum number of individuals of each identifiable species for the collection. This minimum number was thus based on the most frequently counted body part. In contrast to the rock hyrax material, minimum numbers for other prey species were mostly obtained from limb and pelvic bones. Prey items were classified into three major age classes on the basis of the degree of epiphyseal fusion and dental eruption: adult (epiphyses fused); sub-adult (near adult size, epiphyses unfused or fusing); and juvenile (diaphyses and epiphyses still growing). The mass of each prey item was recorded by estimating the proportion of adult mass that the individual represented, and then multiplying this by a figure of mean adult mass. The latter were derived from Skinner & Smithers (1990) for mammals, from Maclean (1985) for birds, and from Branch (1988) for reptiles. An average mass was determined for each species from these estimates of individual mass.

In making separate analyses of each collection from the same site there was the risk that different remains of a single prey captured would be represented in more than one collection from the same site and thus over-represented. This was countered by pooling all remains by site at the end of the study and analysing again for minimum numbers. This was carried out for rock hyrax remains as well, since there was the same possibility of double counting fragments of the same maxillae. Very few pellets were collected beneath nest cliffs (perhaps because they decomposed rapidly), so pellet-analysis was not employed to supplement findings from prey remains.

*Time-lapse photography at eagles' nests* (see previous chapter: pages 147-148).

University of Pretoria etd – Davies, R A G (1994)



*Direct observations of prey on the nests*

Besides trips to change film in the time-lapse cameras, all active nests were normally visited once or twice each year to monitor breeding developments (and to ring chicks in 1987). During the course of the study, about 140 separate visits were made to active nests and most of these were whilst there was a chick in the nest. Each visit I recorded details of the species and estimated age and size of any prey items on the nest. This method could not provide the same volume of information as the time-lapse photography, but at least I could usually obtain a very clear view of the prey through 8,5x45 binoculars. Visits were generally more than ten days apart so the risk of counting the same prey item twice was negligible.

*Direct observations of hunting and feeding behaviour of the eagles*

This method included all sightings of kills (n=15) by eagles; all sightings of eagles carrying freshly-killed prey (n=5); all sightings of eagles delivering freshly-killed prey to nests (n=8); all observations of piracy (n=1); and all observations of eagles scavenging (n=5). These data were derived either during eight separate five-day periods (about 480h) of direct observations on the behaviour of the Lion's Head, Beagle Ravine, Kortkloof and Penberi study pairs; or during 131h of direct observations at active nests belonging to the Sloop and Gamka Dam pairs; or by incidental observation during other activities such as hyrax counts / collection of prey remains, which entailed approximately 567h spent in the veld. Methods employed in the course of direct observations of the behaviour of the study pairs in their territories were described in detail in Chapter 6 (pages 86-87). On two occasions when prey was killed far away, I pinpointed the exact locality of the kill and (with the help of an assistant) later discovered the remains of a karoo korhaan and a suricate at these sites. Some data on black eagle diet derived from direct observations of eagles and of prey on their nests were also obtained from other karoo sites outside the study area.



University of Pretoria etd – Davies, R A G (1994)



## RESULTS AND DISCUSSION

*Factors influencing the collections of prey remains*

Separate analyses of 71 collections of prey remains revealed a total of 3823 prey items identified, most of which were collected from lower escarpment sites (Table 27). Collections at lower escarpment sites were larger

TABLE 27
SIZE AND DISTRIBUTION OF ANNUAL COLLECTIONS OF PREY REMAINS

| | YEAR OF COLLECTION | | | | | |
|---|---|---|---|---|---|---|
| | 1986 | 1987 | 1988 | 1989 | 1990 | TOTAL |
| No. lower escarpment sites | 9 | 11 | 11 | 11 | 5 | 47 |
| No. upper escarpment sites | 3 | 7 | 7 | 7 | 0 | 24 |
| Total no. sites sampled | 12 | 18 | 18 | 18 | 5 | 71 |
| Total no. prey items collected | 881 | 1369 | 742 | 648 | 183 | 3823 |

(mean=63,7; s.d.=66,8; n=39) than collections from upper escarpment sites (mean=36,3; s.d.=27,6; n=24). This difference was statistically significant (Savage Scores Test: $X^2 = 4,2$; $p<0,01$). More prey items were found beneath the nests of birds which bred (mean=80,3; s.d.=73,6; n=30) than beneath the nests of non-breeders (mean=33,9; s.d.=37,0; n=39), and this difference (about 60% less for non-breeders) was highly significant (Kruskal-Wallis Test: $X^2 = 16,2$; $p<0,01$). There was also a significant decline in the number of prey items recovered on consecutive collections as old material was cleared out ($r_p=-0,28$; $p<0,05$), with first collections averaging nearly 90 items, dropping to nearly 40 items by the third collections (Figure 75). About 50 prey items can be expected to be delivered to nests during the 88d nestling period (previous chapter). If the average accumulation rate of prey items under nest cliffs is 40 p.a. then the large initial collections made at some sites (up to 341 items) might reflect diet over the previous seven years. The marked influence of breeding on size of collections is strongly suggestive that collections of prey remains are mostly comprised of prey captured during the nesting season, despite some observations of eagles carrying prey to nesting/feeding sites outside of the breeding season. It was very difficult to search for prey remains on the steep screes and cliffs of the upper escarpment where the eagles have many more rocks to choose from as feeding perches. But smaller samples from these localities might also be associated with the lower breeding rates of upper escarpment pairs (Chapter 6).

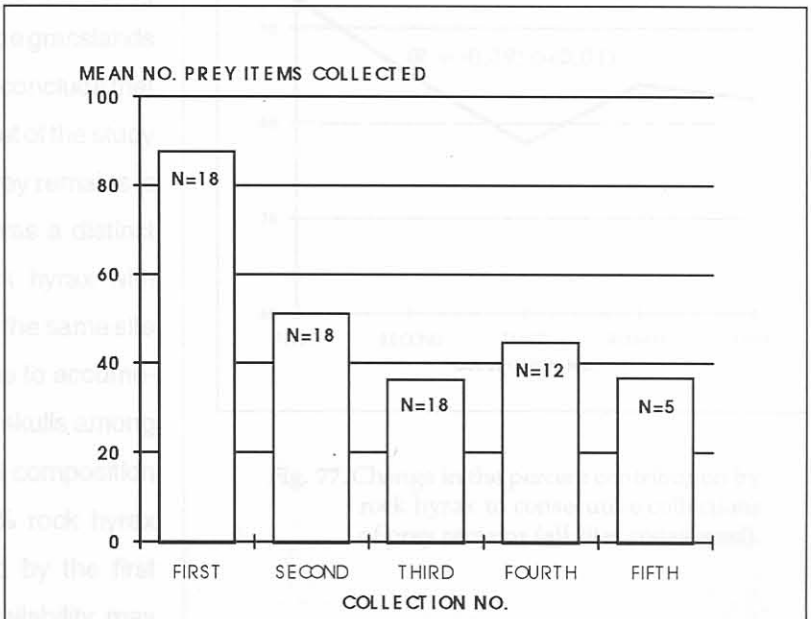



**Figure 75.** recovery of prey items on consecutive collections.

University of Pretoria etd – Davies, R A G (1994)



*Species composition of black eagle diet as indicated by prey remains - in terms of numbers*

The remains of about 40 different potential prey species were found beneath the nest cliffs of the black eagles in and around the KRNP (Table 28). Such a wide spectrum of prey is the product of a large sample size (n=3586 items). Larger collections generally revealed more species fed upon. This is illustrated in Figure 76 which suggests that a sample of about 75 items is needed from a site to give a good indication of the prey spectrum taken. By pooling the samples for each site at the end of the study and re-appraising to avoid the possibility of over-counting a single prey item (this is especially likely with the scutes of a tortoise for instance), sample size was slightly reduced but species composition was not significantly altered. Analyses of the pooled sample are thought to represent the more accurate interpretation of diet. There were minor discrepancies between the two treatments with some re-classifications within the pooled sample.

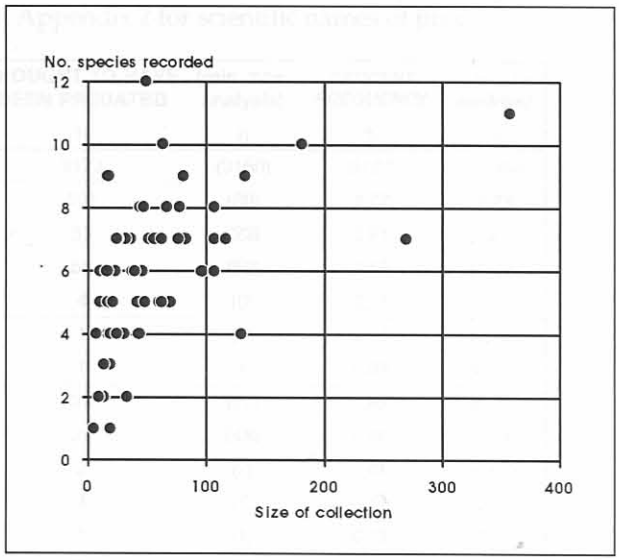



**Fig. 76.** Relationship between the size of the collection of prey remains, and the number of species represented.

Rock hyrax comprised 88% of black eagle prey by numbers. The predominance of rock hyrax in the diet of the study population of black eagles is close to that recorded for the Magaliesberg and the Transvaal (D.G. Allan *in litt.*; Jenkins 1984; Tarboton & Allan 1984), and falls between high levels of dominance in the Matobo Hills (Gargett 1977) and low levels of dominance in the eastern Cape grasslands and the Fynbos (Boshoff *et al.* 1991). I would conclude that the proportion of rock hyrax recorded in the diet of the study population of black eagles as indicated by prey remains is average to high, for this predator. There was a distinct decline however, in the proportion of rock hyrax with consecutive collections of prey remains from the same site (Figure 77). This is thought to be mainly due to accumulation of the large and noticeable rock hyrax skulls among prey remains with time - suggesting that real composition of black eagle diet might approximate 80% rock hyrax rather than 90% rock hyrax as suggested by the first collections. However, changes in prey availability may also have been responsible for the apparent change in dietary composition (discussed later).

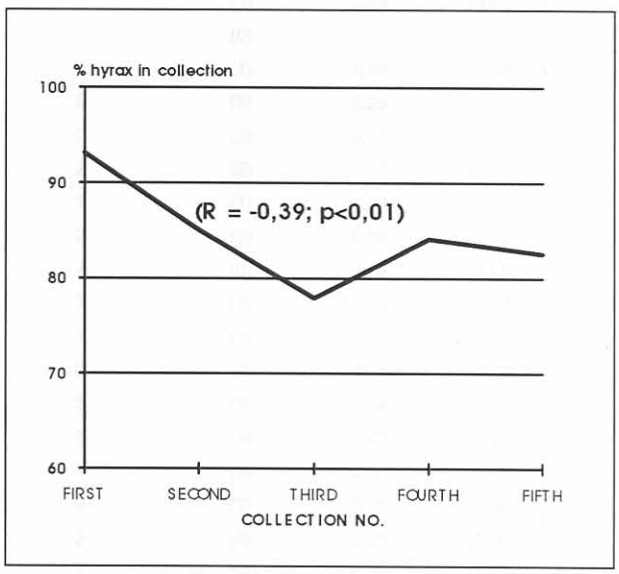



**Fig. 77.** Change in the percent contribution by rock hyrax to consecutive collections of prey remains (all sites considered).

University of Pretoria etd – Davies, R A G (1994)


# TABLE 28

## COMPOSITION OF THE ENTIRE COLLECTION OF PREY REMAINS COLLECTED BENEATH BLACK EAGLE NEST SITES IN AND AROUND THE KRNP

Any item larger than 18kg was considered scavenged rather than predated. Some prey individuals may have been represented twice (by different body parts) in collections from the same sites, so all collections were pooled by site and re-analysed at the end of the study (min. nos. analysis). Consult Appendix 2 for scientific names of prey.

| SPECIES/CATEGORY | CONSIDERED NOT EATEN | POSSIBLY SCAVENGED | (min. nos. analysis) | THOUGHT TO HAVE BEEN PREDATED | (min. nos. analysis) | *PERCENT FREQUENCY* | *(min. nos. analysis)* |
|---|---|---|---|---|---|---|---|
| | n | n | n | n | n | % | % |
| rock hyrax | | | | 3173 | (3150) | *87,07* | *(87,84)* |
| Smith's red rock rabbit | | | | 101 | (80) | *2,77* | *(2,23)* |
| Cape hare | | | | 33 | (23) | *0,91* | *(0,64)* |
| scrub hare | | | | 58 | (50) | *1,59* | *(1,39)* |
| unidentified lagomorph | | | | 4 | (0) | *0,11* | - |
| unidentified rodent | | | | 1 | (1) | *0,03* | *(0,03)* |
| Cape porcupine | | | | 1 | (1) | *0,03* | *(0,03)* |
| steenbok | | | | 23 | (27) | *0,63* | *(0,75)* |
| klipspringer | | | | 29 | (48) | *0,80* | *(1,34)* |
| springbok | | | | 2 | (2) | *0,05* | *(0,06)* |
| mountain reedbuck | | 1 | (1) | 4 | (7) | *0,11* | *(0,20)* |
| grey rhebok | | 3 | (7) | 1 | (1) | *0,03* | *(0,03)* |
| unidentified wild bovid | | | | 3 | (0) | *0,08* | - |
| unidentified domestic bovid | | 37 | (24) | 50 | (40) | *1,37* | *(1,12)* |
| unidentified bovid | | | | 2 | (0) | *0,05* | - |
| suricate | | | | 27 | (26) | *0,74* | *(0,73)* |
| small grey mongoose | | | | 11 | (10) | *0,30* | *(0,28)* |
| yellow mongoose | | | | 3 | (3) | *0,08* | *(0,08)* |
| water mongoose | | | | 1 | (1) | *0,03* | *(0,03)* |
| small-spotted genet | | | | 1 | (1) | *0,03* | *(0,03)* |
| zorilla (striped polecat) | | | | 2 | (2) | *0,05* | *(0,06)* |
| Cape wildcat | | | | 7 | (7) | *0,19* | *(0,20)* |
| bat-eared fox | | | | 1 | (1) | *0,03* | *(0,03)* |
| aardwolf | | 1 | (1) | | (0) | - | - |
| unidentified carnivore | | | | 1 | (1) | *0,03* | *(0,03)* |
| karoo korhaan | | | | 9 | (8) | *0,25* | *(0,22)* |
| helmeted guinea fowl | | | | 2 | (2) | *0,05* | *(0,06)* |
| greywing francolin | | | | 2 | (2) | *0,05* | *(0,06)* |
| African black duck | | | | 1 | (1) | *0,03* | *(0,03)* |
| red-eyed dove | | | | 2 | (2) | *0,05* | *(0,06)* |
| rock pigeon | | | | 7 | (9) | *0,19* | *(0,25)* |
| white-necked raven | | | | 7 | (6) | *0,19* | *(0,17)* |
| black-necked heron | | | | 1 | (0) | *0,03* | - |
| black stork | | | | 2 | (2) | *0,05* | *(0,06)* |
| rock kestrel | | | | 3 | (3) | *0,08* | *(0,08)* |
| large falcon | | | | 1 | (1) | *0,03* | *(0,03)* |
| spotted eagle owl | | | | 1 | (0) | *0,03* | - |
| Cape eagle owl | | | | 2 | (2) | *0,05* | *(0,06)* |
| Ludwig's bustard | | | | 2 | (2) | *0,05* | *(0,06)* |
| Alpine swift | | | | 1 | (1) | *0,03* | *(0,03)* |
| unidentified bird | | | | 2 | (1) | *0,05* | *(0,03)* |
| tent tortoise | | | | 4 | (2) | *0,11* | *(0,06)* |
| greater padloper | | | | 52 | (54) | *1,43* | *(1,51)* |
| leopard tortoise | | | | 3 | (5) | *0,08* | *(0,14)* |
| rock leguaan | | | | 1 | (1) | *0,03* | *(0,03)* |
| TOTAL | 7 | 42 | (33) | 3644 | (3586) | *100,00* | *(100,00)* |
| black eagle | 4 | | | | | | |
| Cape vulture | 3 | | | | | | |

University of Pretoria etd – Davies, R A G (1994)



Carrion comprised just under one percent of the collection if it is assumed that all prey items larger than 18kg were scavenged. If adult and near adult small antelope were also scavenged then carrion would have comprised 1,5% of the prey remains collection.

*Species composition of black eagle diet as indicated by prey remains - in terms of mass*

Average mass for black eagle prey, calculated from estimated mass (see methods) for 3589 prey items was 2565g. Average mass for 2931 rock hyrax taken was estimated to be 2582g (p. 211). Because of the similarity in these two estimates percent biomass of rock hyrax in black eagle diet was not dissimilar from percent frequency. The mean mass for 436 non-hyrax prey of the eagles was estimated to be 2440g. This is lower because small red rock rabbits, carnivores, birds and reptiles made up the majority of non-hyrax prey. It has to be borne in mind that large prey items are more likely to be represented in collections of prey remains than small prey items such as juvenile rock hyrax.

The prey remains suggested that black eagles were catching prey items ranging in size from 200g to 15000g (Figure 78). However 97,3% of prey items taken were estimated to fall into the size range of 500 - 4000g, in close agreement with the estimates of Boshoff *et al.* (1991). Most prey taken are thus smaller than the eagles themselves (mean body mass 3,82kg - see Chapter 8). Juveniles comprised 97% of bovid prey as well as the majority of large carnivores and birds fed upon by the eagles (Table 29).

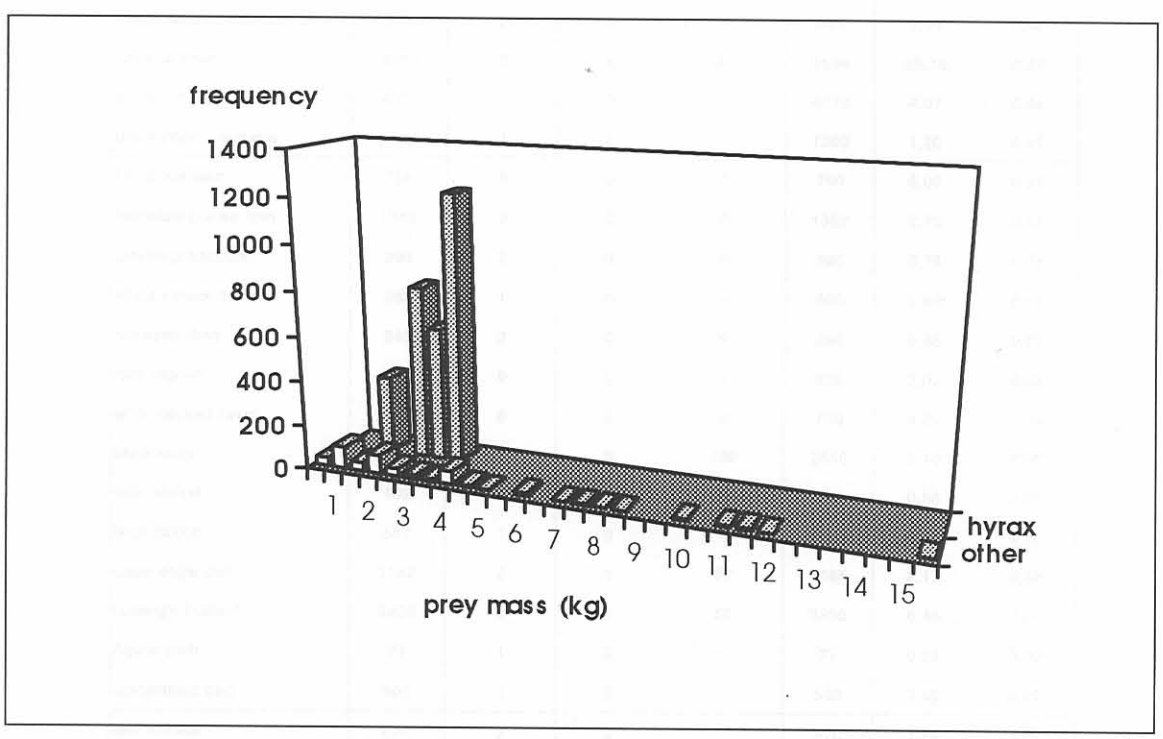



**Figure 78.** Frequency distribution of hyrax and other black eagle prey in accordance with size category, as indicated from 3589 prey remains.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 29

## COMPOSITION OF BLACK EAGLE DIET IN TERMS OF MASS AND THE JUVENILE PREY COMPONENT, AS INDICATED BY PREY REMAINS

Immature prey items were separated on the basis of dental erruption and the degree of epiphyseal fusion. Average mass for each prey species was calculated from mass estimates for each individual (see methods). Consult Appendix 2 for scientific names of prey.

| SPECIES/CATEGORY | ADULT MASS | FREQUENCY | NO. IMMATURE | *(percent immature)* | AVERAGE MASS | BIOMASS | *(percent biomass)* |
|---|---|---|---|---|---|---|---|
| | g | n | n | % | g | kg | % |
| rock hyrax | 3200 | 3150 | 1211 | *38* | 2582 | 8133,30 | *88,43* |
| Smith's red rock rabbit | 1620 | 80 | 13 | *16* | 1541 | 123,28 | *1,34* |
| Cape hare | 2040 | 23 | 2 | *8* | 1983 | 45,61 | *0,50* |
| scrub hare | 3600 | 50 | 20 | *39* | 3268 | 163,40 | *1,78* |
| unidentified rodent | 75 | 1 | - | - | 75 | 0,08 | *0,00* |
| Cape porcupine | 11500 | 1 | 1 | - | 5750 | 5,75 | *0,06* |
| steenbok | 11095 | 27 | 25 | *93* | 4356 | 117,61 | *1,28* |
| klipspringer | 11900 | 48 | 46 | *96* | 5541 | 265,97 | *2,89* |
| springbok | 25000 | 2 | 2 | *100* | 3125 | 6,25 | *0,07* |
| mountain reedbuck | 29400 | 7 | 7 | *100* | 5250 | 36,75 | *0,40* |
| grey rhebok | 20000 | 1 | 1 | - | 2000 | 2,00 | *0,02* |
| unidentified domestic bovid | 38000 | 40 | 40 | *100* | 4180 | 167,20 | *1,82* |
| suricate | 734 | 26 | 1 | *4* | 731 | 19,01 | *0,21* |
| small grey mongoose | 797 | 10 | 0 | *0* | 797 | 7,97 | *0,09* |
| yellow mongoose | 830 | 3 | 0 | *0* | 830 | 2,49 | *0,03* |
| water mongoose | 3400 | 1 | 0 | - | 3400 | 3,40 | *0,04* |
| small-spotted genet | 1900 | 1 | 0 | - | 1900 | 1,90 | *0,02* |
| zorilla (striped polecat) | 843 | 2 | 0 | *0* | 843 | 1,69 | *0,02* |
| Cape wildcat | 4300 | 7 | 4 | *57* | 3594 | 25,16 | *0,27* |
| bat-eared fox | 4070 | 1 | 0 | - | 4070 | 4,07 | *0,04* |
| unidentified carnivore | 1500 | 1 | 1 | - | 1200 | 1,20 | *0,01* |
| karoo korhaan | 750 | 8 | 0 | *0* | 750 | 6,00 | *0,07* |
| helmeted guinea fowl | 1352 | 2 | 0 | *0* | 1352 | 2,70 | *0,03* |
| greywing francolin | 390 | 2 | 0 | *0* | 390 | 0,78 | *0,01* |
| African black duck | 880 | 1 | 0 | - | 880 | 0,88 | *0,01* |
| red-eyed dove | 240 | 2 | 0 | *0* | 240 | 0,48 | *0,01* |
| rock pigeon | 335 | 9 | 0 | *0* | 335 | 3,02 | *0,03* |
| white-necked raven | 700 | 6 | 0 | *0* | 700 | 4,20 | *0,05* |
| black stork | 3000 | 2 | 2 | *100* | 2550 | 5,10 | *0,06* |
| rock kestrel | 192 | 3 | 0 | *0* | 192 | 0,58 | *0,01* |
| large falcon | 587 | 1 | 0 | - | 587 | 0,59 | *0,01* |
| Cape eagle owl | 1142 | 2 | 1 | *50* | 1085 | 2,17 | *0,02* |
| Ludwig's bustard | 3400 | 2 | 1 | *50* | 3230 | 6,46 | *0,07* |
| Alpine swift | 77 | 1 | 0 | - | 77 | 0,08 | *0,00* |
| unidentified bird | 500 | 1 | 0 | - | 500 | 0,50 | *0,01* |
| tent tortoise | 570 | 2 | 0 | - | 570 | 1,14 | *0,01* |
| greater padloper | 510 | 54 | 21 | *39* | 402 | 21,71 | *0,24* |
| leopard tortoise | 12000 | 5 | 5 | *100* | 1080 | 5,40 | *0,06* |
| rock leguaan | 3000 | 1 | 1 | - | 2000 | 2,00 | *0,02* |
| AVERAGE | 5267 | | | | 2565 | | |
| TOTAL | | 3586 | 1405 | *39* | | 9197,88 | *100,00* |

University of Pretoria etd – Davies, R A G (1994)



The calculation of diet composition in terms of biomass is presented in Table 29. The entire collection of prey remains is thought to represent a total prey biomass of 9198kg captured/scavenged by the Nuweveldberg eagles. Comparisons of species composition of black eagle diet in terms of numbers and in terms of mass are summarised in Table 30, and illustrated in Figure 79. When considering diet in terms of biomass rather than frequency, the obvious differences are that large bovid prey take on added importance in fulfilling the food requirements of the eagles at the expense of the smaller carnivores, birds and reptiles. However it should be borne in mind that the product of frequency and mass for each prey species is a simplification of the importance of the prey as food, because eagles are known to consume differing proportions of different sized prey (Gargett 1982a; A.F. Boshoff pers. comm.).

TABLE 30

COMPOSITION OF THE PRINCIPAL PREY TAXA IN BLACK EAGLE DIET IN TERMS OF MASS AND NUMBERS, AS INDICATED BY PREY REMAINS

| PREY | FREQUENCY | *percent* | MEAN MASS | BIOMASS | *percent* |
|---|---|---|---|---|---|
| | n | % | g | kg | % |
| Hyrax | 3150 | *87,84* | 2582 | 8133,30 | *88,43* |
| Lagomorphs | 153 | *4,27* | 2172 | 332,29 | *3,61* |
| Rodents | 2 | *0,06* | 2915 | 5,83 | *0,06* |
| Bovids | 125 | *3,49* | 4766 | 595,78 | *6,48* |
| Carnivores | 52 | *1,45* | 1286 | 66,89 | *0,73* |
| Birds | 42 | *1,17* | 799 | 33,54 | *0,36* |
| Reptiles | 62 | *1,73* | 488 | 30,25 | *0,33* |
| **TOTAL** | 3586 | *100,00* | (2565) | 9197,88 | *100,00* |
| Carrion | (56) | | | | |

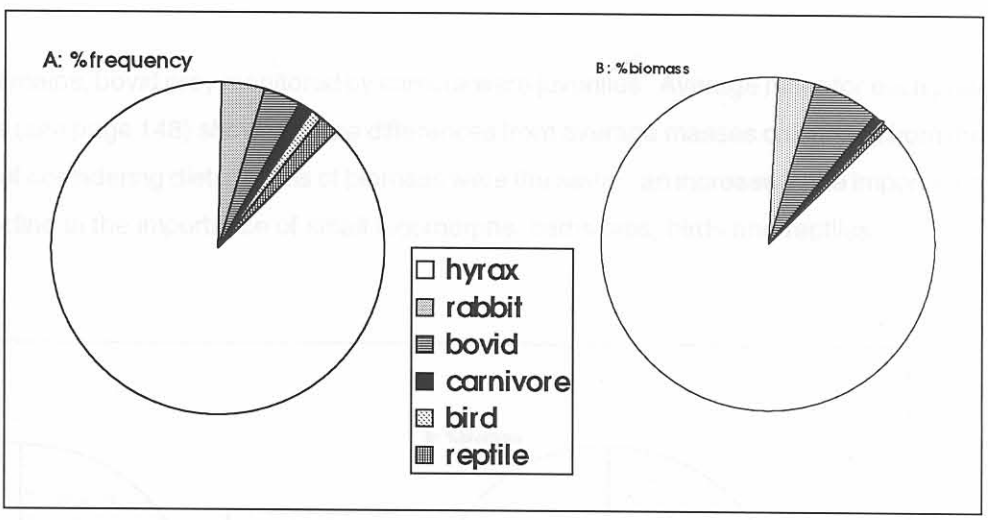



Fig. 79. Percent composition of the principal prey taxa in black eagle diet in terms of frequency (A) and biomass (B), as indicated by prey remains

Average mass calculated for prey items that were considered to have been scavenged by the eagles (i.e. >18kg) was 25,9kg. Taking the frequency of occurrence of carrion in prey remains to vary between 1 and 1,5%, and assuming that 50% of each carcass was monopolised by the eagles (it is actually unlikely that the eagles would consume most of a large ungulate carcass), the contribution of carrion as suggested by prey remains in meeting black eagle food requirements might vary between 4 and 8%. This may be under-estimated because most carrion would be fed on away from the nest cliffs (see later), but the assumption that 50% of each carcass fed on would be monopolised by the eagles is probably very generous. Frequency of scavenging is mentioned again under direct observations, but unfortunately it is not yet possible to be more precise on this aspect of black eagle feeding.

University of Pretoria etd – Davies, R A G (1994)



*Species composition of black eagle diet as indicated by time-lapse photography at nests*

The effectiveness of time-lapse photography as a tool for monitoring black eagle feeding habits was assessed in the previous chapter (page 151). Up to six nests were monitored by time-lapse photography each season over four years, yielding data (average 41d; s.d.=33d) on 17 separate nestling periods. The cameras were placed at the nests of the eagles for a total of 1050 days, during which time they were operational for 82% of the time (864 nest days). Excluding all days before hatching or after fledging, the cameras provided data on 701 days while the eagles were provisioning food to their chicks. A total of 62 films were exposed, which yielded data over an average of 13,5d (s.d.=5,1d) each. At the chosen interval of just over 3,5 min between frames, the films could however comfortably run for 16-17d if no problems were encountered. An average of 206 frames were exposed for each day of filming, and a total of 178000 frames were analysed to yield data on the feeding habits of the eagles.

During the 701 days while the eagles were monitored with chicks, a total of 389 prey deliveries were recorded from the films. Eighty five percent of these prey could be identified, representing 10 species and two unidentified categories, and the composition of black eagle diet that they suggest (in terms of both numbers and mass) is presented in Table 31 and Figure 80. The major prey taxa identified in the collections of prey remains (Table 30) were all represented in the monitored prey deliveries. But there were major differences (tested later) in the proportional representation of the prey by the two methods. Most noticeable was the high representation of red rock rabbits amongst the prey deliveries monitored by camera. Consequently, rock hyrax comprised a smaller fraction (68%) of black eagle diet as indicated by this method.

In accordance with the prey remains, bovid prey monitored by camera were juveniles. Average mass for each prey species delivered to the nests (see page 148) showed some differences from average masses calculated from the prey remains, but the effects of considering diet in terms of biomass were the same: an increase in the importance of large bovid prey, and a decline in the importance of small lagomorphs, carnivores, birds and reptiles.

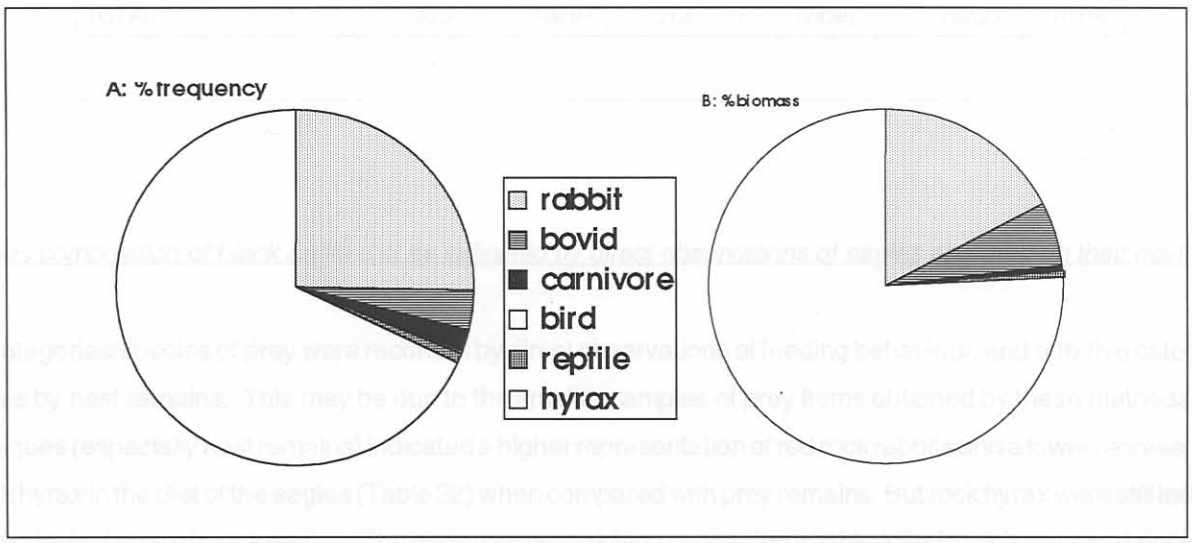



**Figure 80.** Percent composition of the principal prey taxa in black eagle diet in terms of frequency (A) and biomass (B), as indicated by time-lapse photography at nests

University of Pretoria etd – Davies, R A G (1994)



# TABLE 31
## COMPOSITION OF BLACK EAGLE DIET IN TERMS OF MASS AND NUMBERS AS INDICATED BY TIME-LAPSE PHOTOGRAPHY AT NESTS

| PREY | FREQUENCY | *percent* | *Percent juv.* | MEAN MASS | BIOMASS | *percent* |
|---|---|---|---|---|---|---|
| | n | % | % | g | kg | % |
| rock hyrax | 223 | *67,78* | *34,3* | 2691 | 600,09 | *75,75* |
| (unidentified non-hyrax) | (4) | | | | | |
| Smith's red rock rabbit | 67 | *21,16* | *12,5* | 1548 | 103,72 | *13,09* |
| Cape hare | 5 | *1,58* | *50,0* | 1836 | 9,18 | *1,16* |
| scrub hare | 6 | *1,90* | *0,0* | 3600 | 21,60 | *2,73* |
| unidentified lagomorph | 2 | *0,63* | *50,0* | 1133 | 2,27 | *0,29* |
| unidentified rodent | 1 | *0,32* | | 80 | 0,08 | *0,01* |
| steenbok | 2 | *0,63* | *100,0* | 1664 | 3,33 | *0,42* |
| klipspringer | 4 | *1,26* | *100,0* | 2231 | 8,92 | *1,13* |
| unidentified wild bovid | 1 | *0,32* | *100,0* | 1800 | 1,80 | *0,23* |
| domestic bovid | 5 | *1,58* | *100,0* | 6650 | 33,25 | *4,20* |
| small grey mongoose | 3 | *0,95* | | 744 | 2,23 | *0,28* |
| yellow mongoose | 2 | *0,63* | | 830 | 1,66 | *0,21* |
| unidentified viverrid | 1 | *0,32* | | 800 | 0,80 | *0,10* |
| unidentified bird | 1 | *0,32* | | 500 | 0,50 | *0,06* |
| rock leguaan | 2 | *0,63* | | 1400 | 2,80 | *0,35* |
| **SUMMARY:** | | | | | | |
| Hyrax | 223 | *67,78* | *34,3* | 2691 | 600,09 | *75,75* |
| Lagomorphs | 80 | *25,27* | *13,6* | 1710 | 136,76 | *17,26* |
| Rodents | 1 | *0,32* | *0,0* | 80 | 0,08 | *0,01* |
| Bovids | 12 | *3,79* | *100,0* | 3942 | 47,30 | *5,97* |
| Carnivores | 6 | *1,90* | *16,7* | 782 | 4,69 | *0,59* |
| Birds | 1 | *0,32* | *0,0* | 500 | 0,50 | *0,06* |
| Reptiles | 2 | *0,63* | *100,0* | 1400 | 2,80 | *0,35* |
| TOTAL | 325 | *100,00* | *31,5* | (2438) | 792,23 | *100,00* |

*Species composition of black eagle diet as indicated by direct observations of eagles and prey on their nests*

Ten categories/species of prey were recorded by direct observations of feeding behaviour, and only five categories/species by nest remains. This may be due to the smaller samples of prey items obtained by these methods. Both techniques (especially nest remains) indicated a higher representation of red rock rabbits and a lower representation of rock hyrax in the diet of the eagles (Table 32) when compared with prey remains. But rock hyrax were still indicated as the principal prey of black eagles. The birds were seen killing or carrying freshly-killed rock hyrax on 21 occasions, and juveniles comprised six (29%) of these.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 32
## COMPOSITION OF BLACK EAGLE DIET AS INDICATED BY DIRECT OBSERVATIONS AND NEST REMAINS

| PREY | DIRECT OBSERVATIONS OF PREY TAKEN | | | |
|---|---|---|---|---|
| | "Kills or freshly-killed" | *percent* | "Fresh remains on the nests" | *percent* |
| | n | % | n | % |
| rock hyrax | 21 | *60,00* | 40 | *56,34* |
| Smith's red rock rabbit | 3 | *8,57* | 21 | *29,58* |
| Cape hare | 1 | *2,86* | - | - |
| scrub hare | 1 | *2,86* | 3 | *4,23* |
| unidentified lagomorph | - | - | 4 | *5,63* |
| steenbok | - | - | - | - |
| klipspringer | - | - | 1 | *1,41* |
| domestic bovid | - | - | 2 | *2,82* |
| suricate | 1 | *2,86* | - | - |
| unidentified viverrid/rodent | 1 | *2,86* | - | - |
| karoo korhaan | 1 | *2,86* | - | - |
| unidentified bird | 1 | *2,86* | - | - |
| rock leguaan | - | - | - | - |
| piracy | 1 | *2,86* | - | - |
| carrion | 4 | *11,43* | - | - |
| **SUMMARY:** | | | | |
| Hyrax | 21 | *60,00* | 40 | *56,34* |
| Lagomorphs | 5 | *14,29* | 28 | *29,58* |
| Rodents | - | - | - | - |
| Bovids | - | - | 3 | *4,23* |
| Carnivores | 2 | *5,71* | - | - |
| Birds | 2 | *5,71* | - | - |
| Reptiles | - | - | - | - |
| Piracy | 1 | *2,86* | - | - |
| Carrion | 4 | *11,43* | - | - |
| TOTAL | 35 | *100,00* | 71 | *100,00* |

Unfortunately, observations of feeding behaviour were rare (n=35 instances), but out of this small sample size, four observations of eagles feeding on carrion (one springbok; one grey rhebok; and two domestic sheep) is suggestive that scavenging may fulfil a notable amount of black eagle food requirements.

Circumstantial evidence indicated piracy on one occasion: a pair of eagles under observation repeatedly swooped on their neighbours who were perched on the ground out of sight, eventually driving them off; the observation pair then disappeared for 30 min, and when they emerged later the female had a full crop.

University of Pretoria etd – Davies, R A G (1994)



*Comparison of methods*

Annual clearance of prey remains from nest sites which were being monitored by time-lapse photography permitted direct comparison of the results from the two methods for 10 separate nestling periods (periods corresponding to the first collections of prey remains were excluded because these could represent diet before the cameras were operational). These results are presented in Figure 81. Similarity between the results from the two methods was confined to the relative proportions of the minor prey taxa (rodents, bovids and carnivores). It is possible that birds would be consumed rapidly and thus be under-represented by time-lapse photography (see previous chapter).

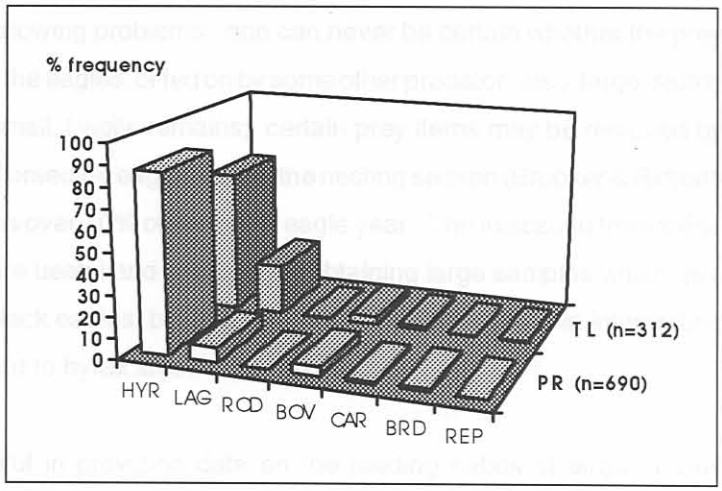



**Fig. 81.** direct comparison of diet composition as determined for ten separate nestling periods using two methods: time-lapse photography at nests (TL) and the subsequent collection of prey remains (PR). Sample sizes refer to the number of prey items observed. Legend: HYR = rock hyrax; LAG = lagomorphs; ROD = rodents; BOV = bovids; CAR = carnivores; BRD = birds; REP = reptiles.

Larger samples of prey items were recorded by the collection of prey remains for each nestling period, although some prey remains may have accumulated during the rest of the year. Prey species diversity was higher (mean=6,6 items) for the prey remains samples than for the time-lapse samples (mean=4,6 items). This difference was statistically significant (t-test for matched pairs: t=2,27; p<0,05). There was a statistically highly significant association between prey type and its representation as determined by the two methods of diet analysis ($X^2$=62,7; p<0,01). In particular, rock hyrax comprised a greater proportion of prey remains (86%) than time-lapse monitored deliveries (68%). These proportions were arcsine-transformed for use in a 2-tailed t-test for matched pairs, and the difference proved to be statistically highly significant (t=3,33; p<0,01). In the same way, there was a statistically highly significant difference between the proportions of red rock rabbits as determined by the two methods (t=3,33; 0<0,01). Red rock rabbits comprised 20% of the time-lapse monitored deliveries and only 3,3% of the prey remains.

Greater species diversity in the prey remains samples is probably due to larger sample size and the ability to accurately identify nearly every bone to species level. The differences in diet composition are considered to be mainly due to under-representation of red rock rabbits and other small prey items in the prey remains samples, rather than their over-representation on the time-lapse films for which no sensible reason could be put forward. Skeletal remains from red rock rabbits are small and fragile, often represented only by a small fragment of the maxilla, or a narrow bone from the hind limbs. These remains are far more likely to pass unnoticed than the obvious skulls left over from rock hyrax prey; and are also far more likely to decompose rapidly. This explanation for the observed differences is borne out by the relatively high representation of red rock rabbits in diet composition as determined by the two other methods: direct observations and observation of nest remains (Figure 82). These two alternate methods did not show the dominance of rock hyrax so characteristic of black eagle prey remains samples. Most

University of Pretoria etd – Davies, R A G (1994)



prey items collected beneath nest cliffs should represent prey of the eagles and give a good indication of diet (Boshoff *et al.* 1990). In the present study this method gave the only comprehensive picture of the diversity of black eagle prey. But collections of prey remains present the following problems: one can never be certain whether the prey represented were killed by the eagles, scavenged by the eagles, or fed on by some other predator; also, large, sturdy prey remains are more likely to be collected than small, fragile remains; certain prey items may be removed by scavengers; and the collection mainly reflects diet of breeding eagles during the nesting season (Brooker & Ridpath 1980) - although this nesting season often comprises over 70% of the black eagle year. The indication from these comparisons of methodology is that prey remains are useful and practical for obtaining large samples which give a qualitative indication of prey spectrum taken by black eagles, but that one has to be very careful in interpreting their quantitative implications, particularly with regard to hyrax:lagomorph ratios.

Time-lapse photography at nests has proved useful in providing data on the feeding habits of large falcons (Enderson, Temple & Swartz 1972; Jenkins 1992) and golden eagles (Lockhart 1976); and can provide the following advantages over collections of prey remains: the method provides direct evidence of prey species fed on by the eagles and can yield useful sample sizes; although there maybe shortcomings with regard to very small prey items (as discussed on page 151), time-lapse photography should give fair representation to all medium and large-sized prey. For these reasons I feel that time-lapse photography gave the best indication of overall ratios between major prey taxa in this study. This method also provided much additional information on feeding habits, notably predation rate (previous chapter).

Composition of the major prey taxa in the diet of the eagles as indicated by all four methods of diet appraisal is illustrated in Figure 82. Occasional observations of prey remains on the nests of the eagles also provide direct evidence of prey species fed on (Collopy 1983b), but cannot give a comprehensive indication of diet composition because of under-representation of small prey items which are consumed rapidly. Observation of nest remains is labour-intensive and cannot provide the bulk of data afforded by the two former methods. Very high representation of red rock rabbits by this method is not easily explained, but may relate to more intensive use of this method in 1989 when rabbits were at peak abundance.

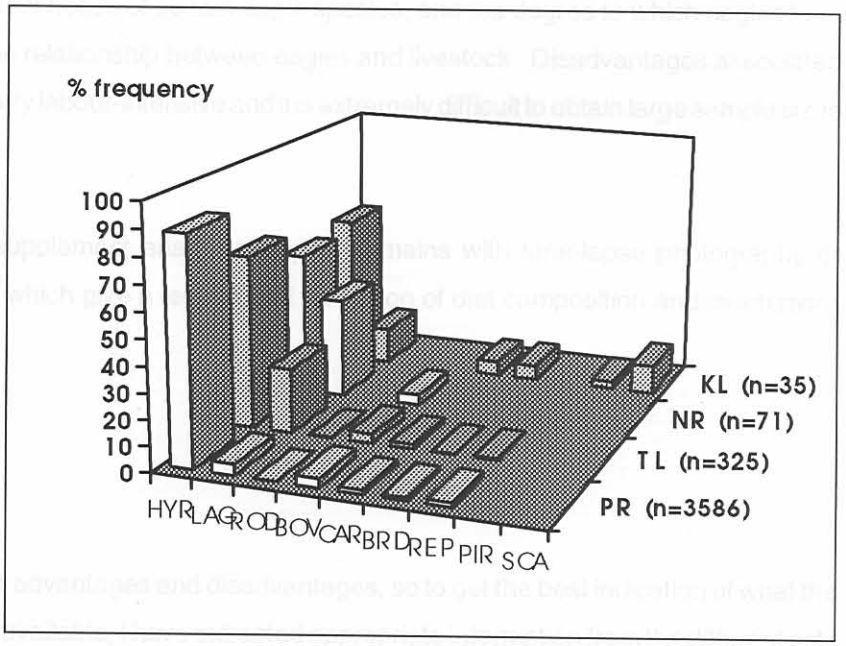



**Fig. 82.** direct comparison of diet composition as determined by four methods: collections of prey remains (PR); time-lapse photography at nests (TL); observation of prey on nests (NR); and kills and other direct observations of eagles feeding (KL). Sample sizes refer to the number of prey items observed. Legend: HYR = rock hyrax; LAG = lagomorphs; ROD = rodents; BOV = bovids; CAR = carnivores; BRD = birds; REP = reptiles; PIR = piracy; SCA = scavenging.

University of Pretoria etd – Davies, R A G (1994)



The three methods discussed so far are all based on the assumption that black eagle diet is accurately reflected in the prey that the birds convey to nesting or feeding sites. Observations of two pairs of eagles conducted over 10 days (116,2h) during the nestling phase indicated that 6 out of 8 prey items captured during this time were actually conveyed to nests. Transport of prey to the nests is necessary during breeding, but regular observations throughout the year of eagles carrying prey suggest that they do prefer to take food to their regular feeding sites. A possible reason for this is that the eagles are able to cache uneaten portions of large prey in safe places.

Intensive observations of the Penberi pair revealed that five meals were carried to such sites (four rock hyrax and one unknown), while three small or large meals were eaten away (karoo korhaan, suricate and springbok carrion). Most rock hyrax prey are small enough to be transported but large enough to last longer than one meal. High representation of adult rock hyrax in nest-based studies of diet may be encouraged by these characteristics. Scavenging from large ungulate carcasses is unlikely to be represented in nest-based studies of diet. Of four observed instances of black eagles scavenging, two of the food items weighed less than 18kg, and only one of these was considered likely to be conveyed to a feeding site. With regard to small prey, three juvenile rock hyrax were taken straight to the nest following capture. Whether small prey items were conveyed to the nest during the nestling period seemed to depend primarily on whether the captor was hungry or not.

The only method which can circumvent all these potential biases in nest-based studies of diet is intensive direct observation of the eagles themselves. This is the only method that can reliably indicate prey captured and eaten away from nest sites, and also the importance of scavenging and piracy in the diet of the eagles. Scavenging and piracy can fulfil a large proportion of the food needs of certain eagle species, and the degree to which eagles feed on carrion has an important bearing on the relationship between eagles and livestock. Disadvantages associated with direct observations are that they are very labour-intensive and it is extremely difficult to obtain large sample sizes of prey eaten.

Studies of eagle diet should evidently supplement analyses of prey remains with time-lapse photography or preferably extensive direct observations, which give a less biased indication of diet composition and much more information on general feeding habits.

*Interpolation of diet*

The four methods of diet appraisal all have advantages and disadvantages, so to get the best indication of what the eagles were eating in relation to what was available, I have extracted appropriate information from the different sets of results.

Time-lapse photography is considered to have given the most realistic indication of overall ratios of rock hyrax : lagomorphs : bovids : carnivores in black eagle prey (estimates of the proportion of rock hyrax in the diet of the eagles were close for all three alternate methods: 59-67%). Birds might be under-represented by this method though, so the ratio of carnivores : birds in the much larger sample of prey remains was used to indicate a likely amount for this

University of Pretoria etd – Davies, R A G (1994)



taxon in the diet of the eagles. Reptiles were very infrequent in the time-lapse sample (n=2; 0,6%), while in the prey remains sample, high representation of this taxon (n=62; 1,7%) was caused mainly by a single nest site. An intermediate value for the amount of reptiles in the diet of the eagles was derived from both methods.

For separating relative abundances of individual prey species within these major prey taxa I used ratios indicated by the much larger prey remains sample. This is based on the assumption that the same bias should affect all lagomorphs, or all carnivores, or all bovids etc. within the prey remains sample. I also felt the prey remains gave a better indication of average prey mass for biomass calculations, because of the much larger samples of each prey species, and because of the opportunity for comparing these prey remains with skeletal material from adults to give a more considered estimate of individual mass.

Estimates for percent frequency and percent biomass in the diet of the eagles calculated in this way are presented for each prey species in Table 33, in order of descending frequency. This summary emphasises the importance of red rock rabbits as alternate prey. This species comprised one in five prey captured, but because of small body mass red rock rabbits fulfilled a reduced proportion of the eagle food needs. Hyrax and lagomorphs are evidently the major prey taxa: together they make up 92% of black eagle prey. I have not included categories for scavenging and piracy because this would be based on too small a sample of observations. However, it should be borne in mind that scavenging could afford the eagles with up to 11% of their food and that piracy can occur.

TABLE 33
PREY COMPOSITION OF BLACK EAGLE DIET
IN TERMS OF MASS AND NUMBERS
AS DETERMINED BY INTERPOLATION OF METHODS

| | % frequency | % biomass |
|---|---|---|
| rock hyrax | 66,73 | 72,64 |
| Smith's red rock rabbit | 21,33 | 13,86 |
| scrub hare | 2,40 | 3,30 |
| klipspringer | 1,43 | 3,34 |
| domestic bovids | 1,19 | 2,10 |
| Cape hare | 1,11 | 0,92 |
| greater padloper | 1,01 | 0,17 |
| suricate | 0,93 | 0,29 |
| steenbok | 0,80 | 1,48 |
| small grey mongoose | 0,36 | 0,12 |
| rock pigeon | 0,32 | 0,05 |
| large wild bovid lambs | 0,30 | 0,57 |
| karoo korhaan | 0,29 | 0,09 |
| Cape wildcat | 0,25 | 0,38 |
| white-necked raven | 0,21 | 0,06 |
| yellow mongoose | 0,11 | 0,04 |
| | | |
| HYRAX | 66,73 | 72,64 |
| LAGOMORPHS | 24,84 | 18,08 |
| RODENTS | 0,58 | 0,22 |
| BOVIDS | 3,72 | 7,49 |
| CARNIVORES | 1,86 | 0,95 |
| BIRDS | 1,11 | 0,42 |
| REPTILES | 1,16 | 0,20 |

University of Pretoria etd – Davies, R A G (1994)



*Species composition of black eagle prey in relation to availability*

The proportion of rock hyrax in the prey remains sample indicated that the dominance of this prey taxon was probably above average when compared to similar studies of diet in other regions. The karoo sample showed highest hyrax dominance for black eagle prey remains collected in the Cape (Boshoff *et al.* 1991). Lower dominance recorded for hyrax in Cape prey remains collections (Boshoff *et al.* 1991; the present study) than in previous studies could partly be due to more detailed analyses of bone fragments at the South African Museum in Cape Town. Only a negligible fraction of old and damaged bones could not be identified to species by comparison with the osteological material housed at the department of Archaeology. The extremely high dominance of rock hyrax (98,2%) in prey remains collected in the Matobo Hills (Gargett 1977) might be lowered somewhat if the large unidentified component of these collections (31%) could be classified in the same way as the Cape material. Over-representation of rock hyrax in collections of black eagle prey remains that may be due to classification bias is further exemplified by the under-representation of small, fragile prey items in these collections as revealed in the present study. One can conclude that most analyses of prey remains probably overestimate the proportion of rock hyrax in the diet of black eagles considerably. In the present study, proportion of hyrax in the diet as indicated by prey remains was 21% higher than that indicated by other, more reliable methods. This difference would have been greater had prey remains only been collected once from each site.

Despite this, rock hyrax made up the major part of black eagle prey as revealed by each of the four methods employed during the present study. As such, this prey taxon can certainly be considered the principal food (Petrides 1975) of black eagles in the karoo region, and makes up nearly three quarters of the biomass of live prey taken by the eagles in the Nuweveldberg. Predation of rock hyrax and other prey species by black eagles in relation to estimates of their availability and abundance are presented in Table 34. From this analysis rock hyrax appear to be taken roughly in proportion to their availability, with an average annual toll by the eagles equivalent to 11,4% of the standing crop.

Eagles apparently showed a higher preference rating for red rock rabbits and other lagomorphs than for hyrax (Table 34). In 1989, it is estimated that the eagles may have been removing as much as 11% of the red rock rabbit standing crop (Chapter 12). Heavy reliance on these prey was unexpected because all lagomorphs in the study area are nocturnal (Skinner & Smithers 1990) and were far less frequently encountered while walking transects than the diurnally active rock hyrax. The ratio at which I encountered rock hyrax to red rock rabbits was about 26 to one. I attributed much of this to the cryptic nature and short flushing distance of the red rock rabbit (Pepler 1990). However, the low profile maintained by red rock rabbits evidently did not protect them from successful predation by black eagles which managed to remove a substantial proportion of the rabbit population each year. Red rock rabbits may have been captured by the eagles while active in the mornings and evenings, or while moving rest sites (page 173). The relatively high toll taken of this nocturnal prey species by the eagles is suggestive that the eagles were hard-pressed to capture rock hyrax.

University of Pretoria etd – Davies, R A G (1994)



# TABLE 34
## PREY TAKEN BY BLACK EAGLES IN RELATION TO ESTIMATES OF THEIR AVAILABILITY AND ABUNDANCE

Frequency of prey in eagle diet was determined by interpolation of methods (see text). Percent availability of prey was determined by transects walked through the veld (Chapter 5). Preference rating was calculated as % frequency in diet / % availability (Petrides 1975). Estimations of standing crop values for prey are explained in Chapters 4 & 5. The annual production of large wild bovid lambs was divided by 12 because these prey were only considered to be vulnerable for their first month. Prey capture rate from Chapter 8.

| | % frequency in eagle diet | % availability in the veld | Preference Rating | Estimated standing crop in a territory | Estimated take by resident pair of eagles | % standing crop removed by eagles |
|---|---|---|---|---|---|---|
| rock hyrax | 66,73 | 69,40 | 0,96 | 1013 | 115,4 | 11,4 |
| Smith's red rock rabbit | 21,33 | 2,68 | 7.96 | 441 | 36,9 | 8,4 |
| scrub hare | 2,40 | 0,38 | 6,32 | 34 | 4,2 | 12 |
| klipspringer | 1,43 | 16,26 | 0,09 | 85 | 2,5 | 3 |
| domestic bovids | 1,19 | - | - | - | 2,1 | - |
| Cape hare | 1,11 | 0,31 | 3,58 | 27 | 1,9 | 7 |
| greater padloper | 1,01 | - | - | - | - | - |
| suricate | 0,93 | 0 | - | - | 1,6 | - |
| steenbok | 0,80 | 2,38 | 0,34 | 12 | 1,4 | 11 |
| small grey mongoose | 0,36 | 1,07 | 0,34 | 16 | 0,6 | 4 |
| rock pigeon | 0,32 | - | - | - | - | - |
| large wild bovid lambs | 0,30 | 2,45 | 0,12 | (4) | 0,5 | 13 |
| karoo korhaan | 0,29 | - | - | - | - | - |
| Cape wildcat | 0,25 | 0,15 | - | 4 | 0,4 | 11 |
| white-necked raven | 0,21 | - | - | - | - | - |
| yellow mongoose | 0,11 | 0,08 | - | 1 | 0,2 | - |
| grey duiker | 0,00 | 0,31 | - | 2 | 0 | 0 |
| Cape fox | 0,00 | 0,15 | - | - | 0 | 0 |
| | | | | | | |
| LAGOMORPHS | 24,84 | 3,37 | 7,37 | 502 | 43,0 | 8,6 |
| BOVIDS | 3,72 | 21,39 | 0,17 | 103 | 6,4 | <6 |
| CARNIVORES | 1,86 | 1,46 | 1,27 | 21 | 2,4 | 11,4 |
| GAME BIRDS | 0,46 | 4,37 | 0,11 | - | - | - |

University of Pretoria etd – Davies, R A G (1994)


Black eagles can undoubtedly detect red rock rabbits better than I, but the high toll taken by the eagles is suggestive that once detected the rabbits were more susceptible to capture than rock hyrax. This is despite apparent territorial behaviour on the part of the rabbit to defend access to rocky shelters (Chapter 5). Evidently anti-predator adaptation for red rock rabbits was not much superior to that for rock hyrax during the circumstances of the present study. Reduced vulnerability of rock hyrax to their main predator is in agreement with theories of co-evolution which predict an evolutionary 'arms race' between predator and prey (Dawkins & Krebs 1979). Rock hyrax certainly do make use of a variety of predator-evasive behaviours notably an early warning system and remaining close to shelter (Chapter 4). When secure in their proximity to shelter, rock hyrax sit boldly on the rocks sometimes even in the presence of predators, so sighting rates of rock hyrax do not necessarily give a true representation of availability. The more obvious behaviour of this prey species probably led to unduly high estimates of its availability from the transect counts. However, if one uses the estimates of prey standing crop in Table 34, rock hyrax also comprise about 70% of the estimated abundance of prey animals.

The local rock hyrax population had just experienced a major decline (Chapters 1, 2 & 4), so the eagles may simply have been hard-pressed to remove more than 11% of the hyrax standing crop each year. Populations of the major alternate prey peaked conveniently in 1989 (see later). Capture of red rock rabbits by black eagles may be a more simple matter of detection, and a substantial removal of standing crop from the rabbit population may also have been facilitated if the rabbits showed a rapid recruitment in response to the 1989 rains.

High representation of red rock rabbits in the diet of black eagles is to be expected on account of the preference of this rabbit for the rocky habitats over which the eagles hunt (Chapter 6), but black eagles also showed an apparent dietary preference for the other lagomorphs in the park (Table 34). Scrub hares are found in tall vegetation throughout the park but their relatively high frequency of occurrence amongst the lagomorph prey might also be favoured by the persistence and noticeability of their large skeletal material in prey remains. Lower preference for Cape hares may be due to their restriction to the arid bottom plains, but the eagles were still apparently removing a significant portion of their population.

Many of the domestic bovid remains found under eagle nests in the KRNP appeared very old, suggesting they represented livestock captured or scavenged before the proclamation of the park (1979-1984). But two thirds of eagle pairs still had easy access to farmland, and time-lapse photography during the field study did not indicate fewer lambs in the diet of the eagles. The indicated toll taken by the eagles (two lambs per territory per year) is low. Black eagle predation of lambs on farms is treated later under geographical variation in diet, and in full detail in Chapter 11.

Wild bovids comprised a much smaller proportion of black eagle diet than lagomorphs or hyrax, but because of their greater size they met relatively more of the eagles' food requirements. Klipspringer were more frequent in the diet of the eagles than steenbok and this is consistent with their predominance in the rocky habitats (Table 13, page 80). But preference rating and the proportion of standing crop removed were much lower for klipspringer than steenbok. This suggests that the eagles were reluctant to attack the larger prey. In fact the eagles exhibited an avoidance for

University of Pretoria etd – Davies, R A G (1994)



all bovids as prey. Adult klipspringer are particularly sturdy animals and can travel at great speed across dangerous rocky terrain. Risk of injury to the eagle must be high when attacking prey such as this, and a relatively minor injury could prove drastic to a predator which relies on great agility in flight. The predominance of juveniles in bovid prey suggests that this is near the upper limit of prey size that the eagles prefer to attack. Relatively low frequency of large wild bovid lambs (e.g. springbok) in eagle diet in comparison to apparent availability may be due to successful defence behaviour by their dams. Such lambs are more likely to be attacked by eagles when isolated or sickly (e.g. McEneany & Jenkins 1983; Bergo 1987; Mooring 1993).

Carnivores, birds, reptiles and rodents were all infrequent in the eagle diet, and because of their small size these prey fulfilled a small fraction of the food needs of the eagles. They do however indicate the versatility of black eagles as predators despite the reputation of this eagle as a specialist. While the population estimates of bovids and carnivores were not calculated rigorously, the relatively large estimates of the standing crop of hyrax, lagomorphs, steenbok and carnivores that are thought to be removed by the eagles each year (Table 34) suggests that this predator is taking advantage of the full range of prey available to it.

Of the carnivores, small grey mongooses were encountered in the veld far more regularly than suricates. Greater frequency of suricates in the diet of the eagles was therefore not expected and may indicate a greater vulnerability of suricates while foraging in groups away from shelter on the bottom plains (pers. obs.).

Pigeons and game birds made up most of the avian prey of black eagles. Capture of avian prey suggests that black eagles can be agile predators, as was observed when a pair of eagles captured a karoo korhaan in flight. The estimation of bird prey in eagle diet was however based mainly on the collections of prey remains, and it is probable that some of the pigeons, white-necked ravens and other birds had died on the cliffs for other reasons. Black eagles are not as manoeuvrable as smaller birds, and capture of avian prey probably depends on a high degree of speed and surprise. Low preference rating for game birds (Table 34), and generally low incidence of avian prey in black eagle diet are indicative that this does not happen very often.

No attempt was made to assess the availability of carrion, and the inferences on the importance of this food source to the eagles are based on questionable assumptions in the case of the prey remains, and small samples in the case of direct observations. Nevertheless the indications are that carrion could fulfil a noticeable portion of eagle food requirements. Scavenging has been recorded for black eagles in South Africa (Frere 1982; Steyn 1982) and both Brown (1988b) and Boshoff *et al.* (1991) report that black eagles readily come to traps baited with carrion. But this feeding behaviour was not observed in the Matobo Hills despite intense work by Gargett (1990) and a team of observers. I think this indicates again that black eagles can adapt to other food sources where these are readily available, and where hyrax may not be.

University of Pretoria etd – Davies, R A G (1994)



*Temporal variation in black eagle diet*

Annual change in the relative contributions of rock hyrax, red rock rabbits and other prey to black eagle diet is shown in Figure 83. An obvious decline in the rock hyrax component of diet was revealed by collections of prey remains between December 1987 and December 1988, and by the time-lapse cameras between 1988 and 1989. Counts at hyrax colonies indicated a significant decline in group size during 1988 (Chapter 4). The change in diet indicated by prey remains tallies with this. However, a decline in the rock hyrax component of prey remains is to be expected with consecutive collections from the same site (first collections made up a significant component of both the 1986 and 1987 samples). It is possible that the observed decline from 91% hyrax to 79% hyrax in the prey remains, was due to both these effects. Summer rainfall at the end of 1987 and at the end of 1988 was below average for both seasons. This undoubtedly hampered recovery of the vegetation following the intense drought of the early 1980's, and is considered responsible for high mortality and low recruitment of hyrax in those years (Chapter 4).

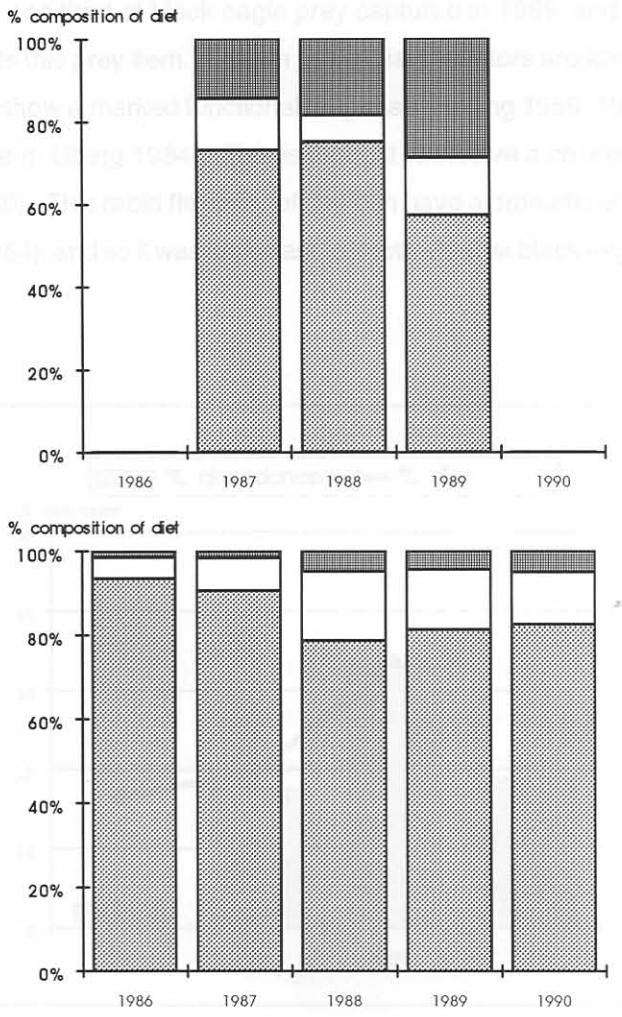



**Fig. 83.** Change in percentage composition of black eagle diet over the study period as indicated by time-lapse photography (top) and collections of prey remains (bottom). (rock hyrax = pale grey; red rock rabbit = dark grey; other prey = white)

Differences in the patterns revealed by the two methods may also result from the inclusion of more food-stressed (see later) upper escarpment eagle pairs in the prey remains collections. The hyrax prey base of these upper escarpment pairs was not monitored and may have been behaving differently from the hyrax populations in the lower escarpment territories. In contrast to the indications from the prey remains, time-lapse photography revealed that the proportion of hyrax in the diet as well as prey capture rate (Chapter 8) were both highest in 1988 for the three years of monitoring . The dry conditions during 1988 may have increased the vulnerability of foraging hyrax, and black eagle predation certainly contributed to the observed decline (Chapter 12), which in turn was reflected in lowest delivery rates of rock hyrax to nests in 1989. Given the limitations of prey remains analyses in representing non-hyrax prey, I think the time-lapse photography (although restricted to lower escarpment nests) gives a more real indication of changes in feeding habits.

University of Pretoria etd – Davies, R A G (1994)



Over the three years of monitoring by time-lapse photography, red rock rabbits became increasingly prevalent as black eagle prey (Fig. 83). This complied with observed increases in the rabbit population which peaked in 1989 (Fig. 40b, page 81). Red rock rabbits comprised nearly one third of black eagle prey captured in 1989, and the noticeable change in diet might indicate a 'switch' towards this prey item. Certain generalist predators are known to subsist on a variety of alternate prey species and can show a marked functional response (Holling 1959, 1965) to feed mostly on one prey when it becomes abundant (e.g. Liberg 1984). This is thought to involve a change in the specific search image of the predator (Tinbergen 1960). This rapid flexibility of diet can have a dramatic effect on predator-prey relationships (e.g. Erlinge *et al.* 1983, 1984), and so it was important to know whether black eagles could be behaving in this way.

Changes in the proportional abundance and proportional predation of red rock rabbits over the study period are shown in Figure 84. If black eagles were showing 'switching' behaviour, one might expect that the change in rabbit abundance would not be as great as the corresponding increase in their contribution to eagle diet. It is clear from Figure 84 however, that this was not the case and it is concluded that the increased predation of red rock rabbits by black eagles did not represent any 'switching' behaviour. After the decline of the hyrax population in 1988, the increase in the red rock rabbits was timely, but the response of the eagles can be described as opportunistic predation that was in proportion to growth of an alternate prey population. The rabbit population was never greater than the hyrax population, so it may be that the increase in rabbits was not sufficient to trigger a switch response.

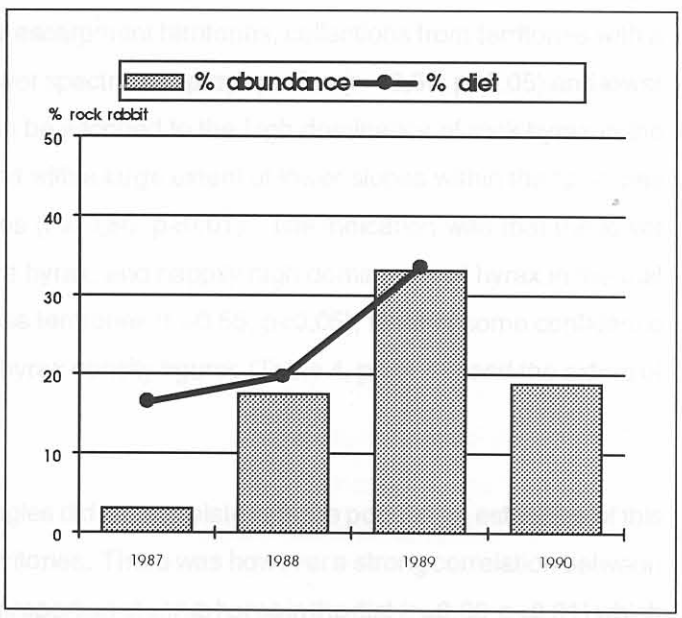



**Figure 84.** Changes in the percentage contribution of red rock rabbits to prey abundance and to eagle diet over the study period. As I was only concerned with ratios of the two main prey species, other prey are excluded from this analysis

In the shorter term, it has been proposed that eagle diet can vary in and out of the nesting period (Boshoff *et al.* 1990). It has been suggested that this can lead to bias in nest-based studies of diet (Brooker & Ridpath 1980). The only reliable indication of black eagle diet during the non-breeding part of the year (February - June), is a small sample of direct observations. These data were compared with direct observations of eagle feeding behaviour during the nesting season (July - January) when I knew the birds were breeding: rock hyrax comprised 14 out of 22 meals (64%) when the birds were nesting, and three out of eight meals (38%) when they were not. This suggestion that the eagles took a wider spectrum of prey when not breeding was not statistically significant. If the eagles chose a different diet when they were obliged to carry food to nestlings, then this should be reflected in a comparison of prey remains collected beneath the nests of birds that bred and beneath the nests of birds that didn't make any breeding effort

University of Pretoria etd – Davies, R A G (1994)



in respective years. All first collections of prey remains, and all collections when breeding attempts failed were excluded from this analysis. Rock hyrax comprised 85,3% of prey items collected beneath the nests of breeders, and 88,2% of prey items collected beneath the nesting and feeding sites of non-breeders. No significant differences in the diet of breeding and non-breeding eagles could be detected.

*Geographical variation in black eagle diet*

Correlation analyses were employed to identify relationships between diet of 17 eagle pairs (as indicated by prey remains) and various characteristics of their territories. Although collections of prey remains were larger under the small cliffs ($r = -0,49$; $p<0,05$) of the lower escarpment territories, collections from territories with a large amount of lower escarpment revealed a narrower spectrum of prey species ($r =-0,50$; $p<0,05$) and lower indices of prey diversity ($r =-0,54$; $p<0,05$). This can be ascribed to the high dominance of rock hyrax in the diet of the lower escarpment eagles which correlated with a large extent of lower slopes within the territories ($r =0,80$; $p<0,01$) and a small extent of upper slopes ($r =-0,80$; $p<0,01$). The indication was that the lower escarpment territories actually accommodated more hyrax, and happily high dominance of hyrax in the diet correlated with population estimates of hyrax in these territories ($r =0,55$; $p<0,05$), lending some confidence to these estimates which had been calculated from hyrax density figures (Table 4, page 48) and the extent of the major topographical habitats in each territory.

The proportion of red rock rabbits in the diet of the eagles did not correlate with the population estimates of this prey derived in a similar fashion for the respective territories. There was however a strong correlation between estimates of red rock rabbits in the territories and the proportion of scrub hares in the diet ($r=0,66$; $p<0,01$) which warrants explaining. The estimates of red rock rabbits were derived from midden densities, so this raises the speculation of whether scrub hare middens could have been mistaken for red rock rabbit middens. Incidental sightings of animals indicated that red rock rabbits outnumbered scrub hares seven to one (Chapter 5). While Smith's red rock rabbits are renowned to make extensive use of middens, scrub hares are not (Skinner & Smithers 1990). So it is very unlikely that scrub hares could have been responsible for many of the middens encountered. Furthermore, the compressed shape of red rock rabbit faecal pellets is diagnostic (Skinner & Smithers 1990) and was checked for during the midden counts. So it is likely that the correlation was spurious. Scrub hares are known to avoid the open plains and prefer tall vegetation (Smithers 1971). The proportion of scrub hare in the diet of the eagles correlated negatively with the extent of the bottom plains in their respective territories ($r =-0,49$; $p<0,05$) and positively with the extent of middle plateau ($r =0,48$; $p=0,05$) and upper slopes ($r =0,49$; $p<0,05$). Tall vegetation in the KRNP grows on the rocky habitats favoured by red rock rabbits. While both lagomorphs might prefer the same broad habitats, only the scrub hares are likely to be fairly represented in collections of prey remains. A similar but opposite association to that with scrub hares was evident between low population estimates of red rock rabbits in eagle territories and high representation of karoo korhaans in eagle diet ($r =-0,49$; $p<0,05$). This correlation reflects the diametrically-opposed preferences of these prey species for the bottom plains habitat.

University of Pretoria etd – Davies, R A G (1994)



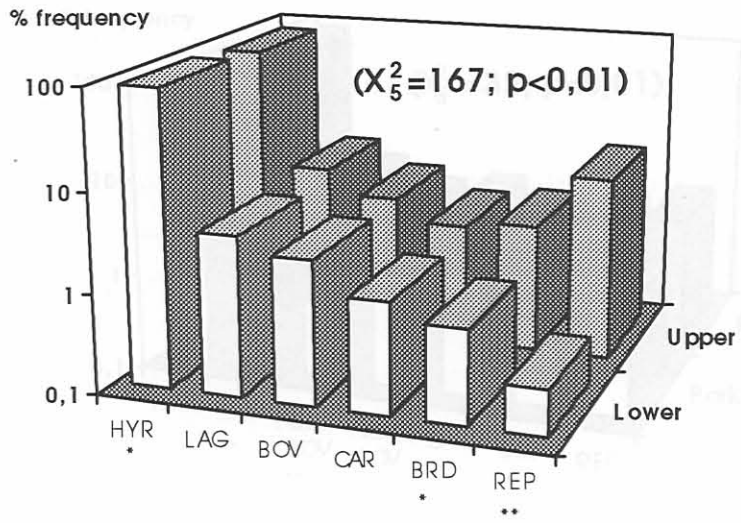



**Figure 85.** Differences in the composition of the major prey taxa represented in collections of prey remains from beneath upper escarpment and lower escarpment black eagle nests sites. Vertical scaling is logarithmic. Asterixes denote differences between the samples that were statistically significant for a Chi-square test (*<0,05; **<0,01).

---

A direct comparison of the diet of upper escarpment and lower escarpment eagle pairs showed a statistically highly significant difference in the representation of the major prey taxa (Figure 85). Birds, especially rock pigeons, featured highly in prey remains collected beneath the tall cliffs (r =0,76; p<0,01) of the upper escarpment, and in territories with a large extent of upper plateau (r =0,82; p<0,01). The proportion of greater padloper tortoise in the diet showed a similar pattern, and was greatest in territories with more upper escarpment (r =0,81; p<0,01). Both these prey species were undoubtedly more available to eagles nesting on the upper escarpment, but it is possible that factors other than eagles were partly responsible for collection of their remains beneath the cliffs. The investigation of black eagle diet in the Cape Province revealed great geographical variation in the importance of birds and reptiles as eagle food, with fynbos eagles taking the greatest quantities of these two taxa (nearly 20% of their diet), and karoo eagles taking the lowest proportions of these taxa in their diet (Boshoff *et al.* 1991).

Another prey species associated with the upper plateau (r =0,80; p<0,01) was Cape wildcat. This may reflect the preference of this predator for high altitude mountains, which was also characteristic of two other small/medium size, generalist predators: jackal buzzards and Cape eagle owls (page 137). By contrast, high representation of small grey mongoose in eagle diet was associated with a large extent of middle plateau in the respective eagle territories (r =0,63; p<0,01). An interesting relationship exists between black eagles and small grey mongooses. This small predator was considered to be responsible for most scavenging beneath eagle nests, and was found responsible for failure rate of eagles nesting on the accessible lower escarpment cliffs through nestling predation (Chapter 6). Predation of red rock rabbits by upper escarpment and lower escarpment pairs was not different and this would comply with an even distribution of this prey through the mountainous habitats, as indicated by the midden counts (Table 10, page 76).

University of Pretoria etd – Davies, R A G (1994)



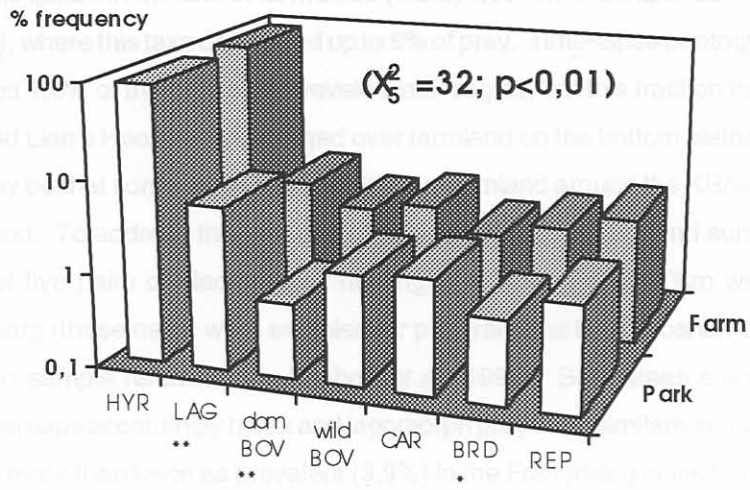



**Figure 86.** Differences in the composition of the major prey taxa represented in collections of prey remains from beneath black eagle nests sites on farm and parkland. Vertical scaling is logarithmic. Asterixes denote differences between the samples that were statistically significant for a Chi-square test (*<0,05; **<0,01).

---

There were differences between the diets of eagles hunting mainly over farmland and those hunting mainly in the park (Figure 86). Farm birds ate relatively more domestic lambs ($X^2$=7,1; p<0,01), more birds ($X^2$=4,0; p<0,05), and less lagomorphs ($X^2$=14,8; p<0,01). Significant correlations were obtained between the extent of farmland in the eagles' territories and the proportions of domestic lamb (r =0,61; p<0,01) and klipspringer (r =0,49; p<0,05) in their respective diet. Most farmland in the study area was situated on the bottom plains frequented by karoo korhaans, or on the upper plateau frequented by rock pigeons. This may explain higher representation of bird prey in farm diet. Red rock rabbits and scrub hares however, mainly occur in the mountainous terrain, and this would explain their predominance in the diet of park birds.

Greater representation of klipspringer in farm diet is puzzling because this species prefers the rocky mountainous habitats. Although a preference for bovid prey amongst farm birds might account for this, it has to be conceded that separation of some juvenile klipspringer material from juvenile domestic bovid material is difficult because the bones of very small juveniles are very similar in shape, so some errors may have arisen here. However, the low frequencies of klipspringer in the diets of both park and farm birds indicate that any under-estimation of domestic lambs in the diet of farm birds through any erroneous classification of material is likely to be by less than 0,76% (of total diet).

There was no indication from diet composition that rock hyrax were less available on farmland. If this is true then farm birds are unlikely to be food-stressed and the abundance of domestic lambs forms an additional, timely food source which can bring the eagles into condition for early breeding (Chapter 6). Approximately 20% of lambs die before weaning, mostly to non-violent causes of death (Chapter 11). So much of this extra food supply may take the form of carrion, and it is likely that farm birds scavenge more than park birds.

University of Pretoria etd – Davies, R A G (1994)



The proportion of domestic lambs in the diet of farm birds (1,6%) was low in comparison with other regions of the Cape (Boshoff *et al.* 1991), where this taxa comprised up to 8% of prey. Time-lapse photography also indicated that domestic lambs comprised 1,6% of the prey of Nuweveld black eagles, but this fraction increased to 3,4% for two eagle pairs (Bakenkop and Lion's Head) which foraged over farmland on the bottom plains and had less access to mountainous areas. It may be that some eagle pairs nesting on farmland around the KRNP were still influenced by the accessibility of parkland. To address this, the diet of eagles nesting on farmland surrounding the KRNP was compared with the diet of five pairs of black eagles nesting in a farmed area 80km west along the Nuweveld escarpment near Fraserberg (these nests were sampled for prey remains by A. Boshoff & G Palmer in 1986, and make up part of the karoo sample referred to in Boshoff *et al.*, 1991). Both areas are characterised by similar escarpment terrain, and perhaps accordingly hyrax and lagomorph prey were similarly represented in the two areas. But domestic lambs were more than twice as prevalent (3,9%) in the Fraserberg collections, suggesting that black eagles may indeed be eating fewer lambs in the vicinity of the KRNP. Unfortunately collections of prey remains do not permit a fuller interpretation of black eagles as stock predators and stock scavengers. These aspects will be taken further in Chapter 11.

*The black eagle as a specialist predator*

An indication of the degree to which black eagles can be considered specialist predators can be obtained by comparing their feeding habits with those of other predators in the same region. Martial eagles occur in the Karoo, often alongside black eagles as was the case in the KRNP. Martial eagles are similar in size and rapaciousness to black eagles, but they are more usually found in flat country. Fortunately extensive work has been done on the diet of both these eagles in the karoo region (Boshoff & Palmer 1980; Boshoff *et al.* 1990; Boshoff *et al.* 1991). The two species took a similar spectrum of prey: 32 prey species were represented in 25 collections of prey remains (n=910) from beneath martial eagle nests in the Karoo (Boshoff *et al.* 1990); while 30 prey species were represented in 31 collections of prey remains (n=3337) from beneath black eagle nests in the Karoo (Boshoff *et al.* 1991). However, individual collections of prey remains from martial eagle sites contained a wider array of species (mean



*Martial eagle attacking helmeted guineafowl*

University of Pretoria etd – Davies, R A G (1994)



8,2; s.d.=2,9) than collections from black eagle sites (mean 6,7; s.d.=2,6). This difference was statistically highly significant (Kruskal Wallis test: $X^2$=14,3; p<0,01), despite the fact that collections at martial eagle sites were usually smaller (mean 36,4 items; s.d.=29,1) than collections from black eagle sites (mean 107,6 items; s.d.=91,8) (Kruskal Wallis test: $X^2$=3,8; p=0,052). To examine intraspecific variation in the diet of both eagles, Boshoff and workers calculated the Shannon-Wiener index of general diversity (Odum 1971: 144) for each site with an adequate sample size. I compared these indices for the two eagle species using a Kruskal-Wallis test and found that collections of prey from martial eagle sites had higher diversity indices (mean 1,64; s.d.=0,27) than collections of prey from black eagle sites (mean 0,57; s.d.=0,37). This difference was statistically highly significant ($X^2$=25,3; p<0,01). While these differences do indicate greater prey-specificity on the part of the black eagle, there are no comparable data for the diversity of prey species available to these eagles, so it is not known whether the differences are caused primarily by the behaviour of the eagles or by variation in relative abundances of the prey. However, hyrax comprised only 52% of prey remains beneath the nest of a pair of martial eagles which had access to the same prey (available to black eagles) in mountainous habitat within the KRNP.

Present findings on black eagle feeding habits suggest that most studies of diet have over-emphasized the importance of rock hyrax. Furthermore, comparisons of predation with prey availability did not indicate a positive preference rating for rock hyrax in the diet of the eagles. In fact the eagles may have been removing equal portions of other prey populations. These observations suggest that black eagles are not obligate predators of rock hyrax, but rather catch the most available prey in mountainous regions.

In apparent contraposition to this, I would argue that these findings still do not refute the notion that black eagles are specialist predators of rock hyrax. At the time of study, local hyrax populations had just experienced a major population decline. The reduced population was probably well protected within the carrying capacity set by the extent of rocky habitat (Chapter 12). Despite this, rock hyrax comprised the major component of black eagle diet in the present study. It is relevant to note that rock hyrax were not represented at all in an analysis of 100 caracal scats collected in the KRNP during the present study (Chapter 7), whereas Palmer & Fairall (1988) found hair of rock hyrax in 22% of caracal scats collected three years previously in the same study area, and this prey is thought to comprise over half of caracal food elsewhere in the Karoo (Grobler 1981; Moolman 1984, 1986a). I think this indicates that, unlike the generalist caracals subsisting on alternate prey, black eagles in the present study were behaving like true specialist predators by pursuing their prey at low density (Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Korpimäki *et al.* 1991). Predation by the eagles was almost the sole mortality agent acting on adult hyrax age classes at this time (Chapter 10).

As specialists, black eagles are evidently highly successful at predating rock hyrax when compared with other predators, but the morphological and behavioural adaptations that enable this (Chapter 6) do not preclude the black eagle from opportune and successful exploitation of other food sources, and this was evident in the high level of predation on an alternative prey species in this study. These observations add to the growing body of literature which shows a high degree of opportunism in black eagle feeding habits when the staple prey is not readily available.

University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 10*

# *BLACK EAGLE FEEDING HABITS -*

# *3. COMPOSITION OF HYRAX POPULATION CLASSES IN THE DIET*

## INTRODUCTION

Numerous studies on predation have shown that particular components of prey populations are more heavily preyed upon than others (e.g. Kruuk 1970, 1972a; Hornocker 1970; Mech 1970; Rudnai 1974; Beacham 1979; Southern & Lowe 1982; Korpimäki 1985b; Donázar & Ceballos 1989; FitzGibbon & Fanshawe 1989; FitzGibbon 1990; Sinclair, Olsen & Redhead 1990). Some theorists have argued that patterns of disproportionate predation of the different prey population components have evolved to harvest the prey population in an optimal way (Slobodkin 1968). More often, there are behavioural traits which explain greater vulnerability and predation of certain population classes (see discussion). Heavier predation (through inferior flight response) can also be expected for any population classes which are less able to maintain a satisfactory body condition, and are thus more likely to become sickly. Smaller prey individuals may suffer heavier overall rates of predation because they are vulnerable to a wider range of predators (Chapter 7). There is little field evidence to suggest that predators actively choose their prey in accordance with an optimal harvest strategy, but there is evidence that predators tend to choose more profitable prey sizes when these are available (Curio 1976).

Different age and sex classes of populations vary with regard to their potential contribution to population growth. Usually young females carry a high potential for reproducing, while old (post-breeding) individuals and surplus males carry low potential. Whether predators actively 'choose' their prey or simply catch the most vulnerable individuals, their demographic influence on the prey is going to vary with the emphasis of their predation in terms of prey population classes. Predators which remove more 'reproductively-valuable' individuals can be expected to exert more demographic and evolutionary influence on their prey than predators which remove more 'reproductively-expendable' individuals. Anti-predator adaptation is only likely to spread amongst the prey population, if it contributes in some way to the likelihood of successful reproduction by a prey individual.

So to fully appreciate the influence of black eagle predation on rock hyrax (involving population modelling - Chapter 12), it was necessary to assess the level of this predation to the resolution of different sex and age classes of the hyrax. Fortunately, accumulations of hyrax cranial and dental material beneath black eagle feeding sites (Chapter 9) permits such detailed analyses. In this chapter, representation of age classes of male and female hyrax in these samples are compared with estimates of their availability among the prey population, and explanations are sought for any patterns of disproportionate predation. The extensive collection of prey remains housed at the South African Museum in Cape Town is used to expand the investigation of temporal and geographical variation in this aspect of black eagle diet. No previous studies on age/sex-specific predation by black eagles have been carried out in any detail.

University of Pretoria etd – Davies, R A G (1994)



## METHODS

Techniques employed in the collection of prey remains from beneath black eagle nesting and feeding sites were described in Chapter 9. Minimum counts of individual hyrax were nearly always obtained from maxillary remains, except in the case of young juveniles in a few samples where mandibles were more numerous. Fourie (1983) recommends that patterns of tooth eruption and tooth wear on maxillae be used for age-determination of hyrax. The high representation of hyrax in prey remains by maxillae was fortunate because it facilitated separation of most individuals by sex and age class. Convenient separation of hyrax skulls or maxillae by sex was facilitated by the high degree of sexual dimorphism evident in the morphology of their upper incisors. These are used by females for feeding, and by males for fighting (Fourie 1983). Males have large, sharply-pointed incisors which are triangular and symmetrical in cross section; whereas females have small converging incisors which are flatter and asymmetric in cross section, with their tips less pointed (Figure 87). Even if these teeth have fallen out, the incisor apertures normally clearly reflect the cross-section of these teeth. This dimorphism is not clear for juvenile animals (Fourie 1983) and so no attempts were made to separate the sexes in the age class 0-1y. Independent observers were employed to check (from incisor/aperture morphology) the sex of 31 skulls of immature and adult hyrax from 'known-sex' animals which had been shot. Ninety seven percent of their predictions tallied with known sex of individuals, with one immature (1-2y old) erroneously classified.

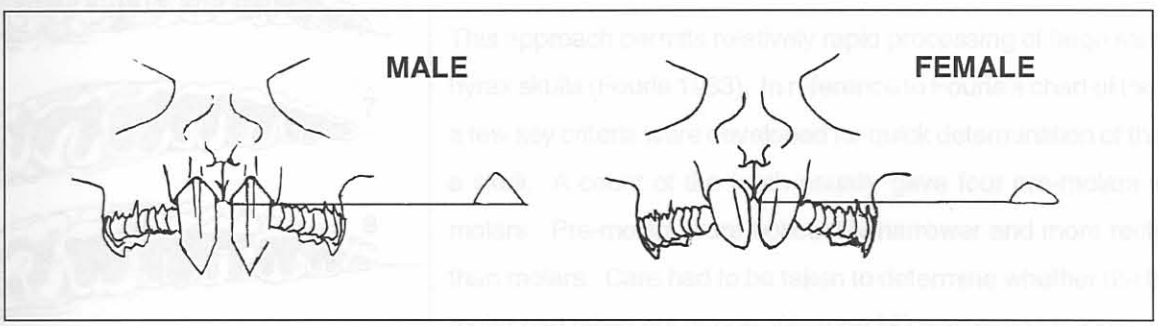



**Figure 87.** Sexual dimorphism for the upper incisors of adult rock hyrax - a head-on view of skulls.

Hyrax maxillae were allocated to annual age classes on the basis of tooth eruption and tooth wear. Adult rock hyrax have four premolars and three molars on each side of the maxilla and the mandibles (Fourie 1983). A certain amount of agreement could be found between three studies on the age-determination of *Procavia capensis* with regard to eruption of these teeth (the following analysis refers to teeth of the maxilla): For rock hyrax at one year old, Fairall (1980), Steyn & Hanks (1983) and Fourie (1983) all agree that incisors have become permanent; that M1 is in wear; and that M3 has not yet appeared. There was some inconsistency between the studies regarding the status of M2 with both Fairall and Steyn & Hanks observing that M2 was visible/erupting, but Fourie noting no sign of M2. I concluded that rock hyrax at one year old showed the following dentition pattern: M1 fully emerged and in wear; M2 may be visible but not in wear; M3 not visible. For rock hyrax at two years of age, all studies reported that both M1 and M2 were emerged and in wear; and all concurred that M3 was in the process of erupting.

University of Pretoria etd – Davies, R A G (1994)



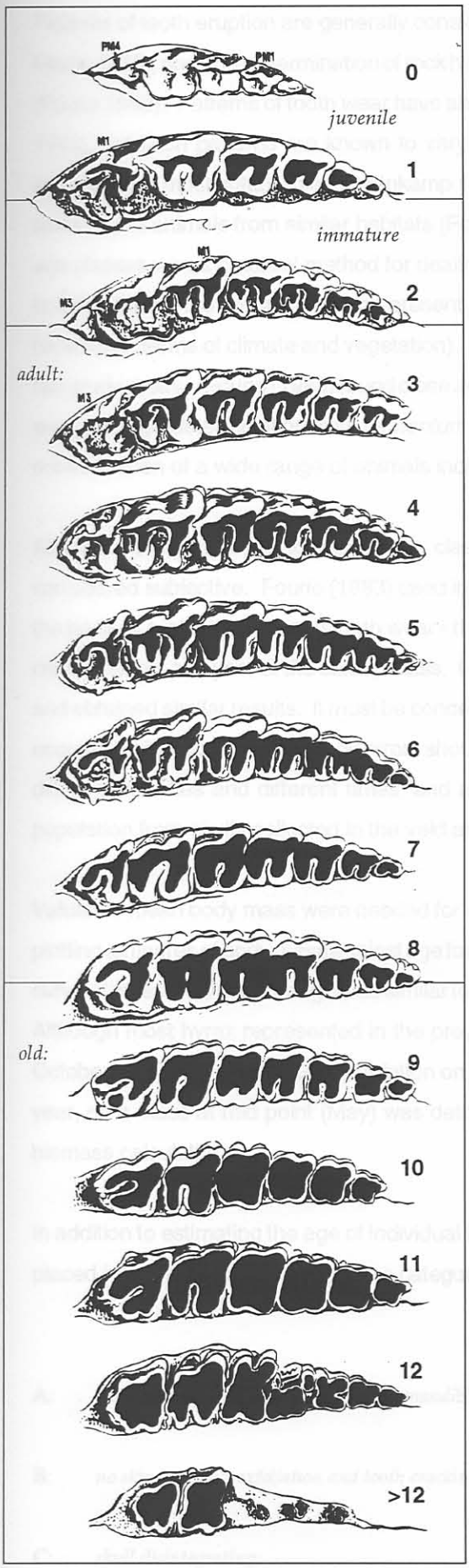



Figure 88. Age-specific patterns of tooth wear for rock hyrax maxillae, from Fourie (1983: Fig. 35). Values to the right of each pattern denote age class in years.

In summary, separation of the first two annual age classes was carried out according to the following criteria: if M2 was not yet emerged and beginning to show signs of wear, the animal was placed in an age class of 0-1y old. If M2 was in wear and M3 was not yet 60% emerged, the animal was placed in an age class of 1-2y old. If M3 had emerged by 60% or more, the individual was considered to be older than two years of age and adult. Subsequent separation of adult hyrax into annual age classes was based mainly on tooth wear patterns observed by Fourie (1983), except that Fourie only recorded wear on M3 at year four whereas the other studies recorded M3 as permanent by 36 months (Fairall 1980), or in wear from 28 months old (Steyn & Hanks 1983). If M3 appeared to be mostly emerged but showed little or no wear and the cusps of all molars appeared very angular and unworn, the individual was classified as 2-3y old. If wear was clearly noticeable on M3, the animal was classified as older than three years and I referred to Fourie's chart of tooth wear (reproduced here as Figure 88) for subsequent separation of the older age classes. Tooth eruption and wear patterns were assumed to be the same for both sexes.

This approach permits relatively rapid processing of large samples of hyrax skulls (Fourie 1983). In reference to Fourie's chart of tooth wear a few key criteria were developed for quick determination of the age of a skull. A count of the teeth usually gave four pre-molars and 1-3 molars. Pre-molars were noticeably narrower and more rectangular than molars. Care had to be taken to determine whether the first pre-molar had fallen out or not. Wear on M3 was used as a key indicator of age, except for young animals as discussed, and for some cases where abnormal jaw structure led to a markedly differential wear pattern on pre-molars and molars - in these cases a compromise was reached between age indicated by wear on molars and age indicated by wear on pre-molars. A good indication of the degree of wear on cusps could be obtained by running a pencil down the central axis of the row of teeth. In accordance with Fourie (1983), the age at which the cusps on these teeth start to merge into a smooth central surface was taken at eight years. From this age on, dental attrition might be associated with senescence so adults were separated from old individuals at this point. Another useful criterion for separating very old animals was the indication from the chart that the 'cutting' ridge on the outside of the teeth was lost at about ten years of age.

University of Pretoria etd – Davies, R A G (1994)



Patterns of tooth eruption are generally considered to give a good indication of an animal's age (Spinage 1973; Hall-Martin 1976), and age-determination of rock hyrax up to three years old by this method is considered to be very accurate (Fourie 1983). Patterns of tooth wear have also been widely used for age-determination in wildlife research (Spinage 1973), but such patterns are known to vary with certain characteristics of the individual being examined and its environment, most notably diet (Steenkamp 1975). So it is recommended that comparisons within species should be restricted to animals from similar habitats (Fourie 1983). Using tooth wear to indicate separation of adult (>3 y old) age classes was a practical method for dealing with large volumes of material in the present study, and its use here is defended on the grounds that the present study, and that of Fourie (1983) were both conducted in similar karoo habitats (in terms of climate and vegetation). One might expect the feeding habits of rock hyrax to be similar in these two study areas. Fourie (1983) found close agreement between age-determination of rock hyrax from tooth eruption/ wear and age-determination from *cementum annuli* in the teeth. The latter is considered a reliable method for age-determination of a wide range of animals including rock hyrax (Grue & Jensen 1979; Fairall 1980).

Allocation of hyrax skulls to annual age classes on the basis of comparison with a chart of tooth wear might be considered subjective. Fourie (1983) used independent, experienced observers to allocate skulls to age classes on the basis of tooth eruption and tooth wear - they placed 70% of skulls in the correct class, and 100% of skulls in age classes within one year of the correct class. I employed observers to independently check my allocations of 25 skulls and obtained similar results. It must be conceded that some discrepancies in age-determination of adults might have occurred using tooth wear, but any errors should have been applied consistently for all collections of prey remains from different localities and different times, and also to estimates of the availability of the different age classes in the population from skulls collected in the veld and from the shot sample (Chapter 4).

Values of mean body mass were needed for each hyrax age class for various calculations. These were obtained by plotting all figures of body mass against age for 59 individuals shot (data summary in Table 6 on page 50). The resultant curve of mass increase with age was similar to that derived in other studies of hyrax growth (Fairall 1980; Fourie 1983). Although most hyrax represented in the prey remains were probably captured during the nestling period (August-October), a similar emphasis of predation on the different hyrax population classes probably applies throughout the year, so a mass at mid point (May) was determined from the growth curve for each hyrax age class to be used in biomass calculations.

In addition to estimating the age of individual hyrax represented in the prey remains (when captured), each skull was placed into one of the following three categories for estimated time since death:

A: *some skin still attached; maxillae and mandibles often still linked; little tooth cracking; no exfoliation of cranium.*

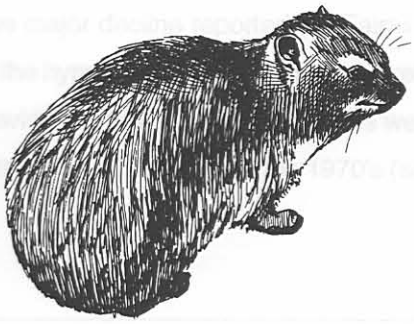
B: *no skin attached; exfoliation and tooth cracking evident but skull structure still solid.*

C: *skull disintegrating.*

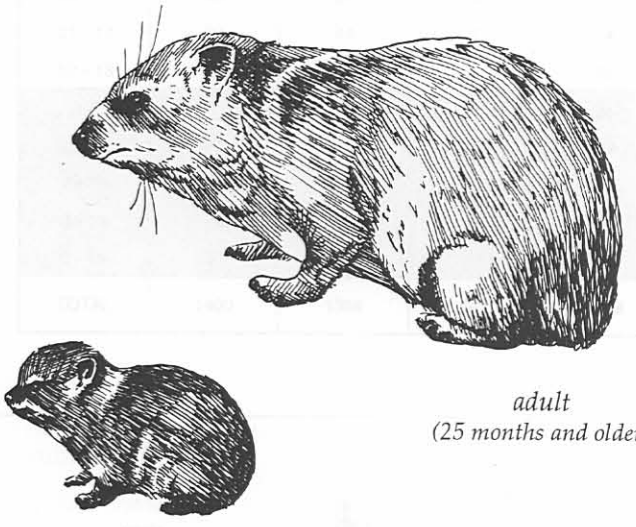
University of Pretoria etd – Davies, R A G (1994)



The object of this exercise was to separate freshly-killed specimens from old material in which larger, stronger skulls may have persisted. From regular observation of hyrax skulls left to decompose in cages (to exclude scavengers), it became clear that nearly all skulls placed in the first category would represent animals killed within the year preceding the collection. Care was taken not to place skulls which were thought to have been well preserved for longer than a year in a micro climate of soil or vegetation into category A. Some allowance was also made for faster decomposition of the more fragile juvenile skulls. Most flesh and skin disappeared from the experimental carcasses by about six months depending on the action of invertebrates. Exfoliation and cracking of the cranium and teeth could begin within a year of death if the skull was exposed to direct sunlight. Disintegration of adult skulls was thought to commence after about two years in exposed conditions. Additional information recorded for each skull was whether the cranium had been opened by the eagles (in the occipital region) or not, or whether this was indeterminable (e.g. disintegrating skulls). Hyrax teeth were checked for any plant material lodged between the cusps which might indicate that these individuals had been foraging when captured. Gargett (1990) noted such evidence for a hyrax delivered to a Matobo eagle nest. However, very few skulls examined in the present study showed any such evidence, and no real conclusions could be drawn from these examinations because it is likely that most plant material would have disintegrated or washed away prior to collection.



*immature*
*(13 months old)*



*adult*
*(25 months and older)*

*juvenile*
*(1 month old)*

University of Pretoria etd – Davies, R A G (1994)



*Overall composition of rock hyrax captured*

Between 1986 and 1991 a total of 3359 hyrax skulls or maxillae were collected beneath black eagle nesting and feeding sites in the KRNP. Sexual dimorphism was evident for 87,5% of the sample excluding juveniles. Allocation to annual age classes was possible for 91,6% of the sample. The overall composition of this sample is presented in Table 35 and Figure 89.

Despite suspicions that large hyrax skulls would be over-represented amongst the older material collected, the composition of only the freshly-killed material (category A) was not very different (Figure 90). However it is not known whether the older material was taken from a population with a different composition from that during the study period. On account of the major decline reported (N. Fairall *in litt.*, 1991) for the hyrax population, this seems likely, and there is evidence that Cape black eagles were catching relatively more juveniles in the 1970's (see later).

TABLE 35

COMPOSITION OF ALL HYRAX SKULLS/MAXILLAE COLLECTED BENEATH BLACK EAGLE NESTING SITES IN AND AROUND THE KRNP DURING THE STUDY PERIOD

Skulls/maxillae of indeterminable sex are placed in the 'unknown' column. Disintegrating skulls could not always be allocated to annual age classes but could usually be placed in a larger age grouping (shaded rows).

| AGE CLASS (y) | MALES | FEMALES | UNKNOWN | TOTAL |
|---|---|---|---|---|
| 0 - 1 | - | - | 372 | 372 |
| 1 - 2 | 418 | 322 | 81 | 821 |
| 2 - 3 | 198 | 155 | 23 | 376 |
| 3 - 4 | 121 | 113 | 15 | 249 |
| 4 - 5 | 111 | 109 | 21 | 241 |
| 5 - 6 | 73 | 72 | 12 | 157 |
| 6 - 7 | 72 | 79 | 14 | 165 |
| 7 - 8 | 89 | 90 | 7 | 186 |
| 8 - 9 | 81 | 102 | 8 | 191 |
| 9 - 10 | 58 | 73 | 6 | 137 |
| 10 - 11 | 48 | 34 | 5 | 87 |
| 11 - 12 | 29 | 44 | 1 | 74 |
| 12 - 13 | 8 | 10 | - | 18 |
| < 2 | 1 | 4 | 20 | 25 |
| 2 - 8 | 31 | 29 | 58 | 118 |
| 2 - 13 | 5 | 10 | 30 | 45 |
| 8 - 13 | 10 | 11 | 8 | 29 |
| 0 - 13 | 2 | 2 | 61 | 65 |
| TOTAL | 1400 | 1398 | 561 | 3359 |

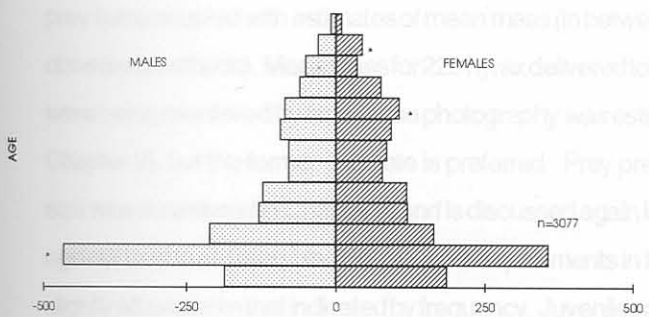



Fig. 89. Population structure of all classifiable hyrax skulls/maxillae (n=3077) collected beneath black eagle nests in and around the KRNP during the study period. Asterixes denote age classes where sex ratio differed significantly (p<0,05) from parity. (youngest age class at the bottom)

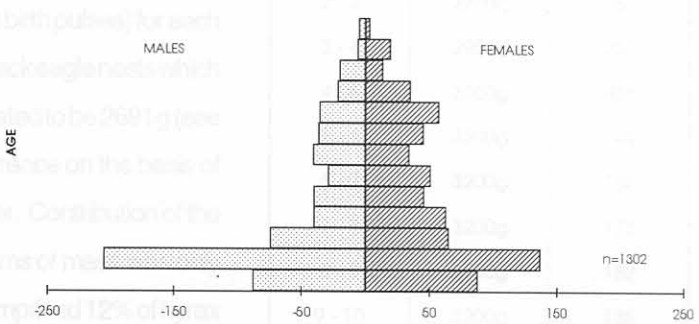



Fig. 90. Population structure of all fresh (category A) classifiable hyrax skulls/maxillae (n=1302) collected beneath black eagle nests in and around the KRNP during the study period.

University of Pretoria etd – Davies, R A G (1994)



A direct comparison of freshly-killed (category A) and older (categories B + C) skulls collected at the end of 1987 (this was the largest collection, and contained many 'first-time' collections from nesting sites), only provided a slight indication that skulls of the very oldest individuals might be more prevalent amongst the more ancient material (Figure 91); and there was certainly no suggestion that juveniles were under-represented amongst the older material. However, the dynamic nature of hyrax population structure (Chapter 4), may well preclude such comparisons from portraying such bias in the methodology.

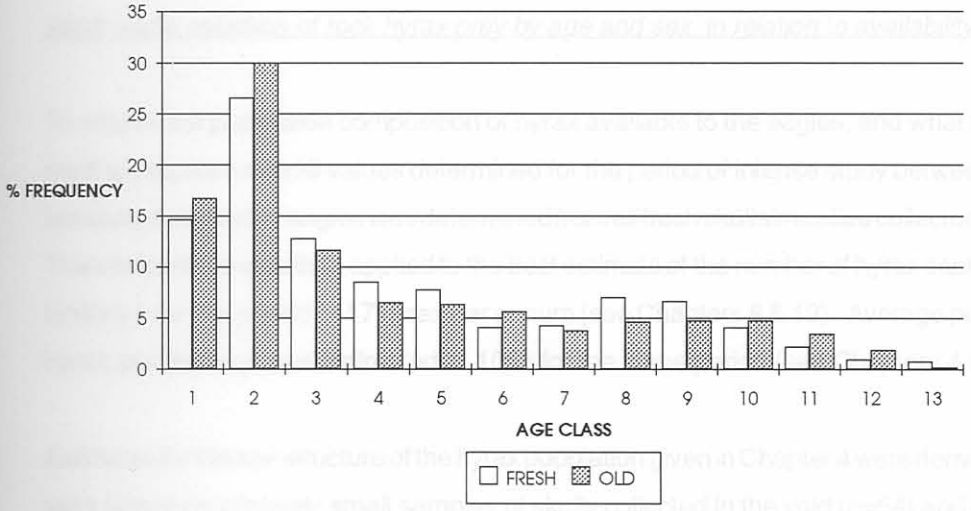



**Fig. 91.** Percent frequency representation of the annual age classes by fresh (category A) and older (categories B & C) hyrax skulls/maxillae from one large collection of prey remains from black eagle nesting sites in and around the KRNP at the end of 1987.

Whether considering only freshly-killed material or the entire sample, the general pattern of composition was the same. Immature hyrax (1-2y old) comprised 27% of the entire collection of skulls, and greatly outnumbered juveniles or any other age class in eagle diet. There was a general trend for younger age classes to be represented more frequently in the sample, but 7-9y olds outnumbered 5-7y olds.

In Table 36 a mean mass of 2582g is derived from the age structure of 2931 hyrax prey items coupled with estimates of mean mass (in between birth pulses) for each class (see methods). Mean mass for 223 hyrax delivered to black eagle nests which were being monitored by time-lapse photography was estimated to be 2691 g (see Chapter 9), but the former estimate is preferred. Prey preference on the basis of size was considered in Chapter 9, and is discussed again later. Contribution of the age classes to meeting black eagle food requirements in terms of mass was only slightly altered from that indicated by frequency. Juveniles comprised 12% of hyrax captured but they only comprised 5% of the hyrax biomass consumed. It should be borne in mind that juvenile maxillae might be under-represented in the collections of prey remains. The relative contribution by immatures was slightly reduced in terms of mass, while that of adult and old age classes was slightly increased.

TABLE 36
MEAN MASS AND FREQUENCY OF THE HYRAX AGE CLASSES REPRESENTED IN THE PREY REMAINS

| AGE CLASS (y) | MEAN MASS (in May) | FREQUENCY |
|---|---|---|
| 0 - 1 | 1100g | 348 |
| 1 - 2 | 2150g | 779 |
| 2 - 3 | 2700g | 362 |
| 3 - 4 | 2950g | 237 |
| 4 - 5 | 3100g | 235 |
| 5 - 6 | 3200g | 149 |
| 6 - 7 | 3200g | 158 |
| 7 - 8 | 3200g | 175 |
| 8 - 9 | 3200g | 182 |
| 9 - 10 | 3200g | 135 |
| 10 - 11 | 3200g | 86 |
| 11 - 12 | 3200g | 71 |
| 12 + | 3200g | 14 |
| | mean 2582g | total 2931 |

University of Pretoria etd – Davies, R A G (1994)



Overall sex ratio for the entire sample was extremely close to parity (Table 35). The entire collection of skulls was used for comparisons of each age class by sex, on the basis that freshly-killed material did not present a noticeably different picture, and assuming that male and female skulls belonging to the same age class decompose at the same rate. There was a statistically significant association with sex for certain age classes ($K_{11}^2 = 24,0; p < 0,05$). In particular, males were more predominant in the immature class ($K_1^2 = 5,7; p < 0,05$), while females comprised significantly more 8-9y olds ($K_1^2 = 4,2; p < 0,05$), and significantly more 11-12y olds ($K_1^2 = 4,0; p < 0,05$).

*Black eagle selection of rock hyrax prey by age and sex, in relation to availability*

To assess the population composition of hyrax available to the eagles, and what they were taking from it, I used the most appropriate overall values determined for the period of intense study between 1987 and 1990. Composition of hyrax captured by the eagles was determined from all fresh skulls/maxillae collected at the end of 1988, 1989 and 1990. This composition was then applied to the best estimate of the number of hyrax captured by black eagles in an average territory over this period - 117 hyrax per annum (see Chapters 8 & 12). Average post-reproductive population size for hyrax, per territory, was estimated at 1062 for the same period (see Chapters 4 & 12).

Estimates for the age structure of the hyrax population given in Chapter 4 were derived from life table calculations which were based on relatively small samples of skulls collected in the veld (n=54) and of animals shot (n=52). Estimates for the composition of the toll taken by the eagles were derived from a much larger sample (n=955). The skulls collected in the veld (away from known black eagle feeding sites) were thought to represent mortality other than that attributable to black eagles. Constructing an age structure for the population from these skulls proved inappropriate when it was discovered that black eagles accounted for the majority of adult and old hyrax that died (see later). This problem became manifest when I found that for a few older female age classes, the estimated toll taken by the eagles (which I have more confidence in) exceeded the estimated total mortality of that class, which had been calculated from the life tables (effects of a declining hyrax population had been taken into consideration when constructing the life tables).

These discrepancies were dealt with in the following manner: a simulated stable hyrax population was created on a computer spreadsheet (MICROSOFT EXCEL 4.0). Initially, overall mortality rates described in Chapter 4 were used for both males and females, but these were then adjusted in order to satisfy conditions that were observed. These conditions, the source of observations on which they were based, and the extent to which they could be satisfied in the model are presented in Table 37. The initial cohort and subsequent sex-specific mortality rates were manipulated to give a best fit for the model in meeting the observed conditions. I was not able to satisfy all conditions exactly. For instance, it was difficult to reconcile observed mortality rates with estimates of composition. This was probably caused by the variety of sources of observation, some of which represented the population at slightly different times. Also, the simulated population represents a population where the numbers dying in any age class conform to a fixed composition of age classes, and this composition remained stable over at least 50 birth pulses. In reality, recruitment and mortality varied dramatically on an annual basis (Chapter 4). This led to a noticeable decline in the hyrax population during 1988 and a partial recovery thereafter. So the spreadsheet simulation can only be regarded as a simplified

University of Pretoria etd – Davies, R A G (1994)



# TABLE 37

## PRE-DISPOSING CONDITIONS FOR THE SIMULATION OF AN ARTIFICIAL ROCK HYRAX POPULATION - THE SOURCE OF THEIR OBSERVATION, AND THE DEGREE TO WHICH THEY COULD BE SATISFIED IN THE MODEL

| PRE-DISPOSING CONDITIONS | SOURCE | MODEL |
|---|---|---|
| Total population should approach 1062 individuals | Counts and colony plots (chapter 4) | 1061,7 |
| Juveniles should comprise @35% pop. | Counts at colonies (juveniles might have been slightly underestimated) | 40,6% |
| One-year olds should comprise @18% | Counts at colonies | 16,2% |
| Two-year olds should comprise @12% | Life tables from veld skulls and shot sample | 9,9% |
| 3-7 year olds should comprise @29% | Life tables from veld skulls and shot sample | 27,7% |
| Old individuals (8-13y olds) should comprise @6% | Life tables from veld skulls and shot sample | 5,7% |
| Adult sex ratio should approach 1male:1,2 females due to heavier male mortality between one and three years old | Shot sample & Fourie (1983) | 1:1,20 |
| Mean litter size should approach @2,53 | Shot sample, Millar (1971), Fourie (1983) | 2,44 |
| About 79% of females should be pregnant | Shot sample | 78,5 |
| Juvenile mortality rate should approach @0,55 | Counts at colonies & Fourie (1983) | 0,60 |
| Overall adult + Immature mortality rate should approach @0,30 | Counts at colonies | 0,27 |
| Age specific mortality rates for adult and old ahyrax were based on those derived from life tables, but a few were adjusted to accomodate black eagle depredations (more reliable data) | | |
| Age specific fecundity rates were derived from Fairall et al. (1986) & Fourie (1983), and adjusted to conform with observations on litter size and pregnancy rate (see above). | | |

caricature of this situation but it is my best estimate of overall hyrax population composition and mortality rates across the study period. It certainly provides a more comprehensive indication of population composition and process than that presented in Chapter 4.

University of Pretoria etd – Davies, R A G (1994)



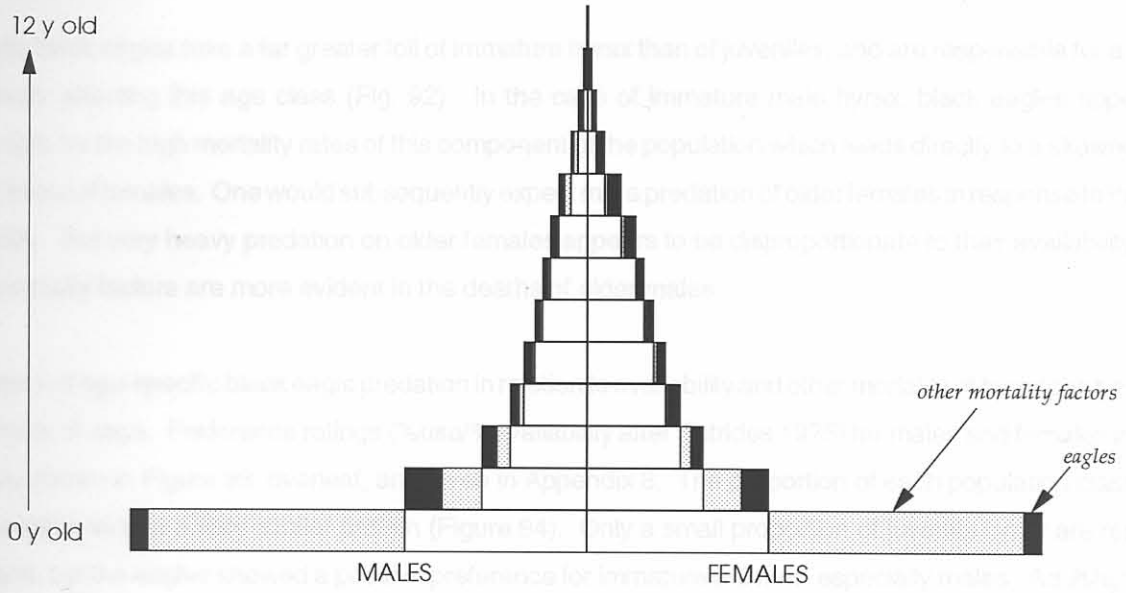



**Figure 92.** A diagramatic summary of age- and sex-specific predation by black eagles in relation to the availability and the annual mortality of the hyrax population classes. This summary was derived by computer simulation of a stable hyrax population which best represents the population under study - see text for method.

The model is summarised diagrammatically in Figure 92, showing age and sex-specific predation by black eagles in relation to the availability and mortality of hyrax population classes. This summary really represents an annual 'snapshot' of the hyrax population during the period of study. The diagram emphasises that black eagles are not an important mortality agent for juvenile rock hyrax. By use of a hyrax population model, Swart *et al.* (1986) emphasised that juvenile mortality was the most important parameter affecting rock hyrax population dynamics in the MZNP, but the highest values for juvenile mortality (84%) that were used in their model were not observed in nature. Starvation and disease were considered to be the main factors causing this juvenile mortality, but it has been shown in Chapter 7 that predation of this age class should not be ignored. Predators normally take a high toll of juvenile prey (e.g. Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990), probably because juveniles often react in a naive fashion to predators (Fourie 1983; pers. obs.) and may not be able to flee as effectively as older animals.

The toll of juvenile hyrax taken by black eagles in the present study may have been under-estimated if this age class was under-represented in collections of prey remains. Skulls of small juveniles may be entirely consumed by the eagles, so this seems likely. Direct observations of eagles hunting or feeding on hyrax suggested that the proportion of juveniles amongst hyrax captured (29%) might be twice that indicated by the collections of prey remains (12-15%). But this is based on a very small sample (n=21) of observations (Chapter 9). Time-lapse photography actually indicated that only 13% of all hyrax delivered to black eagle nests (n=223) were estimated to weigh less than or half adult mass when intact (this would correspond to the size of the first age class). Even if black eagles were capturing twice as many juveniles as indicated by the prey remains, this would still only represent a minor part of the juvenile mortality. The juvenile age class might be somewhat under-represented in calculations of age structure of the prey remains sample, but this should not unduly affect estimates of the toll taken from the older age classes because the juvenile component may also have been slightly under-estimated in the investigations of prey capture rate based on time-lapse photography (Chapter 8).

University of Pretoria etd – Davies, R A G (1994)



Evidently black eagles take a far greater toll of immature hyrax than of juveniles, and are responsible for a major part of mortality affecting this age class (Fig. 92). In the case of immature male hyrax, black eagles appear largely responsible for the high mortality rates of this component of the population which leads directly to a skewed adult sex ratio in favour of females. One would subsequently expect more predation of older females in response to their greater availability. But very heavy predation on older females appears to be disproportionate to their availability (Fig. 92). Other mortality factors are more evident in the deaths of older males.

The pattern of age-specific black eagle predation in relation to availability and other mortality of hyrax can be presented in a number of ways. Preference ratings (%use/%availability after Petrides 1975) for males and females in each age class are shown in Figure 93, overleaf, and given in Appendix 8. The proportion of each population class removed by the eagles reveals a very similar pattern (Figure 94). Only a small proportion of juvenile hyrax are removed, as discussed, but the eagles showed a positive preference for immature animals, especially males. Adult hyrax appear to be taken roughly in proportion to their availability with no obvious preference for either sex (just over 10% of these classes are removed by the eagles each year). But animals older than 7y are evidently heavily preyed upon. Just under one third (32%) of all old hyrax in the population were removed by the eagles each year. Eagles showed the highest preference ratings for these older prey animals, especially females.

The high preference ratings for females indicates that heavy predation of these classes is not just a response to greater availability. Females were noticeably preferred by the eagles in each of the older age classes except the 10-11y olds. Unfortunately, hyrax of this age only comprise a tiny fraction of the population, so the shift might be an artefact caused by small sample sizes. But most 10-11y old hyrax captured by the eagles between 1987 and 1989 would have been born around 1978. A relationship between sex and rainfall during the estimated birth year is described later and in Chapter 4. Greater availability of males born or recruited in the dry year of 1978 conforms to this relationship. A shift in the availability of the sexes amongst 10-11y olds may well have been lost in the calculations of population structure. Estimates of selection by the eagles were not modified or smoothed in any way, so the shift in preference towards male 10-11y olds might reflect errors in the estimates of availability.

Black eagles were a major mortality agent for all age classes except juveniles. Eagles accounted for 45,2% of the immature hyrax that died each year; 67,1% of the adult hyrax that died; and 64,6% of old animals that died (Figure 95). Between ages 7 to 10y old, other mortality factors appear to affect males, while black eagles were mostly responsible for female deaths in these age classes.

Black eagles were evidently responsible for most post-juvenile mortality of the hyrax population. It is conceivable that such 'hard' selection pressure would encourage co-evolution between prey and predator. But the present study represented a hyrax population at low density being pursued by a specialist predator (Chapter 9). These conditions may be associated with the maximum pressure that predators can exert upon their prey (Pearson 1966, 1971; Fitzgerald 1977). So extrapolating to the level of historic species interaction can only be speculative. In other regions such as the Mountain Zebra National Park, black eagles may be nest-site limited, and other predators may have more influence on rock hyrax populations (Swart *et al.* 1986).

University of Pretoria etd – Davies, R A G (1994)



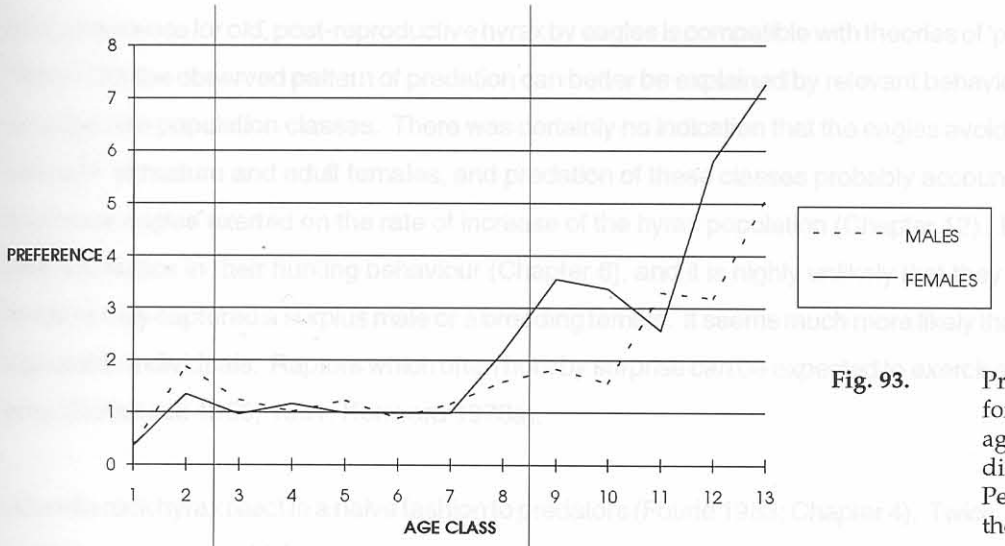



**Fig. 93.** Preference ratings by black eagles for male and female rock hyrax age classes - calculated as percent diet/percent availability, after Petrides (1975). Vertical lines down the page separate immature, adult and old age classes. Consult Appendix 8 for values.

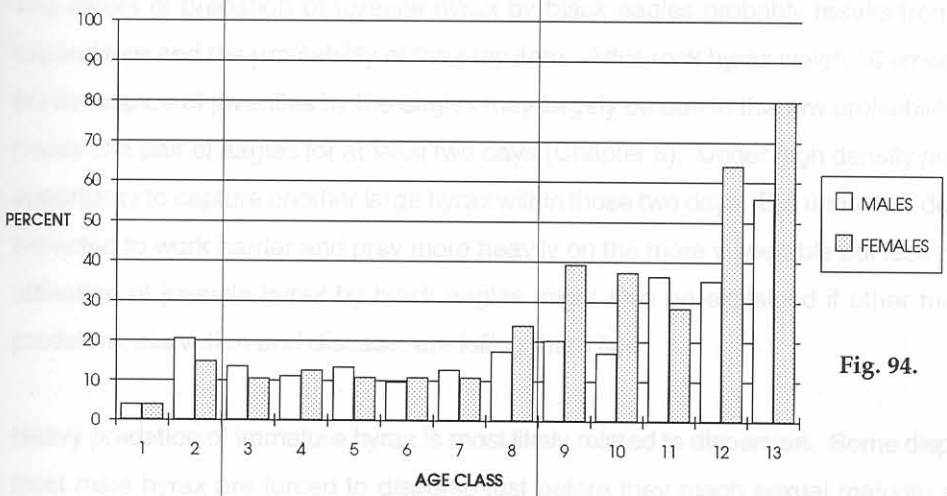



**Fig. 94.** The estimated proportion of each hyrax population class removed annually by black eagles.

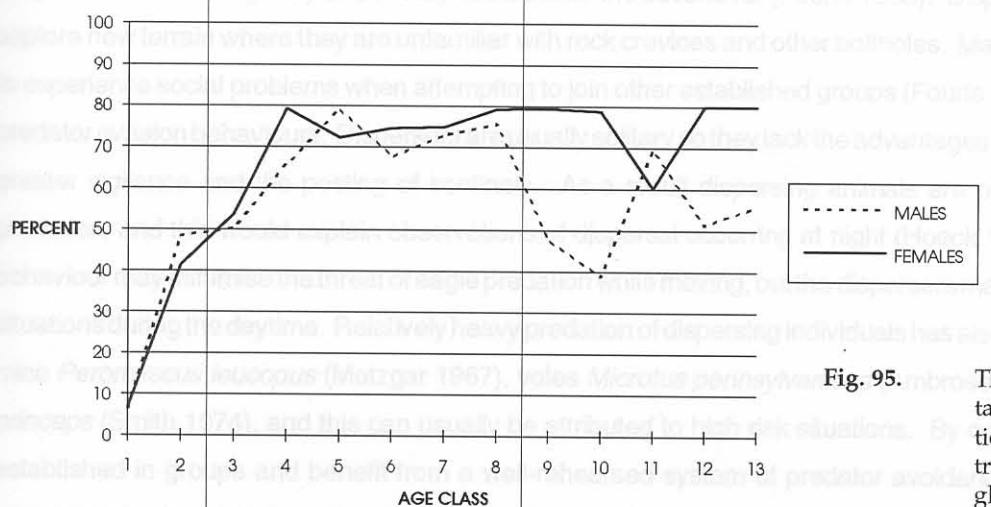



**Fig. 95.** The estimated proportion of mortality affecting each hyrax population class annually, that can be attributed to predation by black eagles.

University of Pretoria etd – Davies, R A G (1994)



High preference for old, post-reproductive hyrax by eagles is compatible with theories of 'prudent' predation (Slobodkin 1968). But the observed pattern of predation can better be explained by relevant behaviour affecting the vulnerability of respective population classes. There was certainly no indication that the eagles avoided the more 'reproductively-valuable' immature and adult females, and predation of these classes probably accounted for most of the influence that black eagles exerted on the rate of increase of the hyrax population (Chapter 12). Black eagles usually employ surprise tactics in their hunting behaviour (Chapter 6), and it is highly unlikely that they would exercise control over whether they captured a surplus male or a breeding female. It seems much more likely that they simply catch the most vulnerable individuals. Raptors which often hunt by surprise can be expected to exercise less selective effect on their prey (Rudebeck 1950, 1951; Kenward 1978a).

Juvenile rock hyrax react in a naive fashion to predators (Fourie 1983; Chapter 4). Twice, black eagles were observed to capture juveniles which took refuge in bushes instead of crevices when the sentinel sounded the alarm. Juveniles are probably easier to catch than older hyrax, but they are highly precocious at birth and very agile at escaping over rocks, so their capture does not necessarily incur much less energy expenditure on the part of the eagles, per strike. The extent of predation of juvenile hyrax by black eagles probably results from a trade-off between this energy expenditure and the profitability of the prey item. Adult rock hyrax weigh 16 times the mass of young juveniles. So the avoidance of juveniles by the eagles may largely be due to this low profitability. A large hyrax can fulfil the food needs of a pair of eagles for at least two days (Chapter 8). Under high density prey conditions there may be ample opportunity to capture another large hyrax within those two days. But under low density conditions the eagles can be expected to work harder and prey more heavily on the more vulnerable but less profitable juveniles. Relatively low utilisation of juvenile hyrax by black eagles might also be explained if other mortality factors such as generalist predators, starvation and disease, are killing them first.

Heavy predation of immature hyrax is most likely related to dispersion. Some dispersion occurs in the first year, but most male hyrax are forced to disperse just before they reach sexual maturity at their second rut (Fourie 1983). Although under low density conditions some adult, non-territorial males may be tolerated within a social group in a sexually quiescent state (Hoeck *et al.* 1982; Van der Merwe & Skinner 1982; Chapter 4). Dispersion of females is less frequent and less obligatory and mostly occurs after the second rut (Fourie 1983). Dispersing animals are forced to explore new terrain where they are unfamiliar with rock crevices and other boltholes. Males especially are more likely to experience social problems when attempting to join other established groups (Fourie 1983) and this may influence predator evasion behaviours. Dispersers are usually solitary so they lack the advantages of group-living, which include greater vigilance and the posting of sentinels. As a result dispersing animals are probably highly vulnerable to predation, and this would explain observations of dispersal occurring at night (Hoeck 1982; pers. obs.). Nocturnal behaviour may minimise the threat of eagle predation while moving, but the dispersers may still find themselves in risky situations during the daytime. Relatively heavy predation of dispersing individuals has also been noted for white-footed mice *Peromyscus leucopus* (Metzgar 1967), voles *Microtus pennsylvanicus* (Ambrose 1972), and pikas *Ochotona princeps* (Smith 1974), and this can usually be attributed to high risk situations. By contrast, most adult hyrax are established in groups and benefit from a well-rehearsed system of predator avoidance and daily routine. Unlike younger animals, adults know how to evade eagles, and their behaviour towards such predators cannot be considered naive. Reduced vulnerability of adult hyrax to black eagles is therefore to be expected.

University of Pretoria etd – Davies, R A G (1994)



It is generally accepted that old animals become less alert to danger and less able to escape predators. Deterioration in these behaviours may be directly caused by senescence. But these effects are likely to be aggravated by loss of body condition in association with dental attrition, which in rock hyrax occurs after eight years (Fourie 1983). Dental attrition may necessitate changes in foraging behaviour which result in more time spent away from shelter. These explanations are offered to account for the very high preference for old hyrax shown by black eagles in the present study. Relatively heavy predation of old animals is often reported in predation studies of higher vertebrates (Hornocker 1970; Kruuk 1970, 1972a; Mech 1970).

The disproportionately high predation of old female hyrax in comparison with old males may be due to a tendency amongst older females to accept high-risk sentinel behaviour (Chapter 4). Sentinels were clearly highly vulnerable to predation while running to catch up with foraging groups, usually when the groups had disappeared into riverine scrub. At this stage the sentinel did not have the advantage of others looking out for it, and usually ran the whole length down to the river, rather than pausing at temporary shelters as the others had done. But relatively less predation of older males may also be due to greater involvement of other factors in the deaths of old males. Intra-specific aggression is more often recorded for male rock hyrax than for females (Fourie 1983). This aggression can take the form of vicious contests over territory or harem ownership, and the wounds inflicted can lead to the deaths of the individuals involved (Fourie 1983). Territorial male hyrax may be most susceptible to this mortality in late adulthood when they are displaced.

Hoeck *et al.* (1982) and Fourie (1983) suggested that non-breeding 'peripheral' adult male hyrax which are loosely associated with harem groups may suffer heavier rates of predation and act as a buffer to the breeding colony. A similar role is suggested for sub-ordinate, non-breeding individuals among springbok *Antidorcas marsupialis* (Bigalke 1970), and among red grouse *Lagopus scoticus* (Jenkins *et al.* 1964). In most social organisations, males are more likely to be forced into such situations than females, and this probably explains why many studies indicate disproportionately heavier predation of males (e.g. Rudnai 1974; Beacham 1979; Korpimäki 1985b; Sinclair *et al.* 1990). In the case of hyrax, it would appear that heavier predation of males is confined to the immature age class.

Much of the age and sex-specific vulnerability of hyrax can be expected to peak at particular times of the year. It is thus possible to predict when particular prey categories should become more important in the diet of the eagles. For instance, juveniles might be more heavily predated between November and March when they are more abundant and show more naive behaviour towards predators. Immature males should be more heavily preyed upon when dispersing before the rut in February and March; while immature females should be more heavily preyed upon after the rut in winter. One would expect adult hyrax to suffer greater predation at those times of year when body condition is at its worst for their respective sex. For males, this occurs during the rut (April); while for females this occurs during lactation in November and December (Fourie 1983). Such effects are likely to be influenced by rainfall patterns and the food supply. Annual collections of prey remains may be slightly biased by these variations in vulnerability, and they do not permit any testing of these predictions. However, they do allow other investigations of variation in the selection of different hyrax population components by black eagles over longer time periods.

University of Pretoria etd – Davies, R A G (1994)



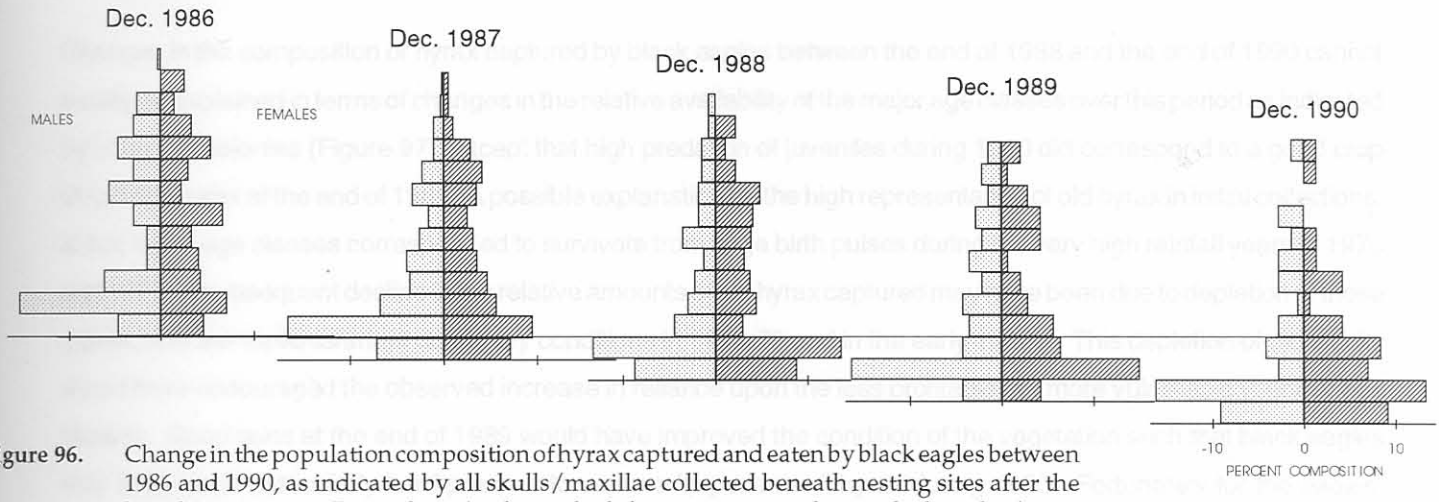



**Figure 96.** Change in the population composition of hyrax captured and eaten by black eagles between 1986 and 1990, as indicated by all skulls/maxillae collected beneath nesting sites after the breeding season in December. (males to the left, youngest age class at the base line)

*Annual variation in the age and sex composition of rock hyrax captured by black eagles*

The composition of hyrax preyed upon by black eagles over the five annual collections is shown diagrammatically in Figure 96. Trends in the selection and availability of four major age classes during the study period are summarised in Figure 97, and were tested for any change. There was a statistically highly significant change in the crude age composition of hyrax taken by black eagles over the study period ($K_{12}^2 = 26{,}9; p < 0{,}01$). In particular, juveniles showed a significant ($K_4^2 = 10{,}7; P < 0{,}05$), erratic change which resulted in an overall increase during the study period; whilst old animals showed an opposite trend ($K_4^2 = 11{,}3; p < 0{,}05$). Representation of immatures in collections of prey remains showed a steady increase but none of this change was statistically significant. Adults comprised the most consistent portion of hyrax age classes in prey remains over the study period. Mean age of hyrax captured by black eagles in 1986 was 4,8y; by 1990 this had dropped to 3,4y.

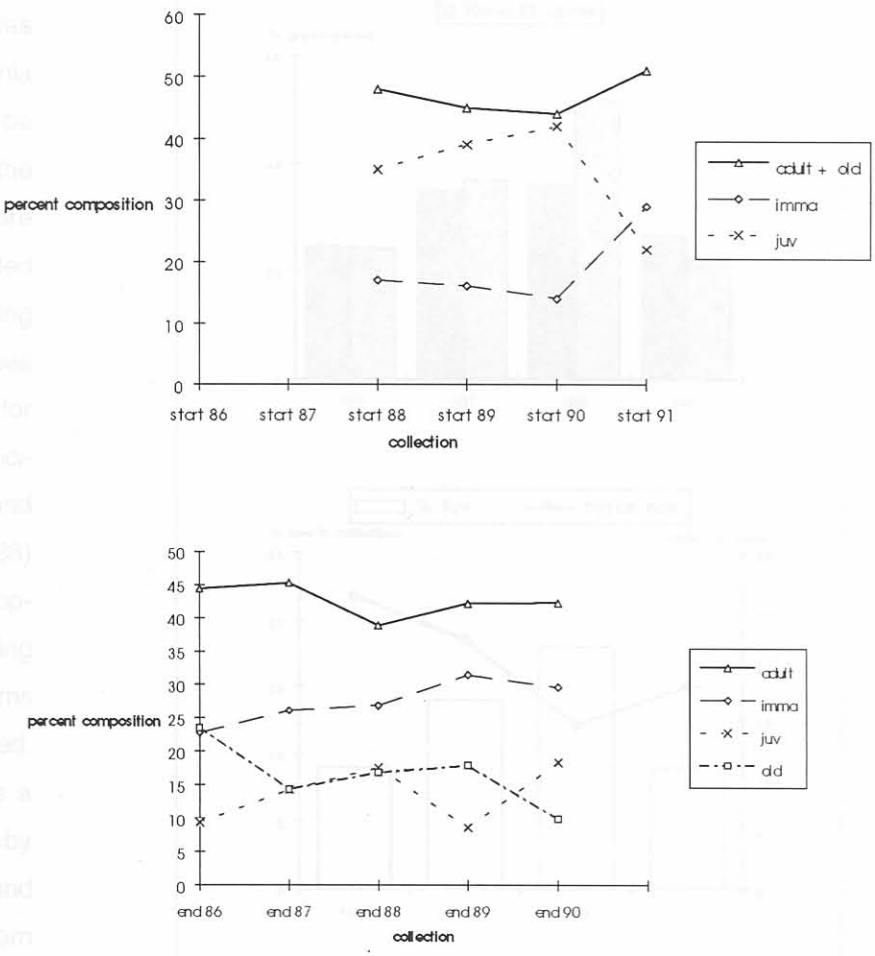



**Figure 97.** Year to year changes in the composition of the major hyrax population components available to the eagles (above - from colony counts) and taken by the eagles (below - from prey remains), over the study period.

University of Pretoria etd – Davies, R A G (1994)



Changes in the composition of hyrax captured by black eagles between the end of 1988 and the end of 1990 cannot readily be explained in terms of changes in the relative availability of the major age classes over this period as indicated by counts at colonies (Figure 97); except that high predation of juveniles during 1990 did correspond to a good crop of juvenile hyrax at the end of 1989. A possible explanation for the high representation of old hyrax in initial collections, is that these age classes corresponded to survivors from large birth pulses during the very high rainfall years of 1976 and 1977. A subsequent decline in the relative amounts of old hyrax captured may have been due to depletion of these stocks, and low replenishment during dry conditions in 1978-79 and in the early 1980's. This depletion of old stocks would have encouraged the observed increase in reliance upon the less profitable but more vulnerable younger age classes. Good rains at the end of 1989 would have improved the condition of the vegetation such that black eagles may have been particularly hard-pressed to capture 'experienced' hyrax during 1990. Fortunately for the eagles, alternative prey species were more available by this time, so the eagles were able to partly compensate for this by capturing a greater portion of other prey species (Chapter 9).

The pattern of increase in the juvenile component of hyrax captured by black eagles was closely mirrored by the amount of hyrax crania opened by the eagles (Figure 98). It may be that this correlation results merely from the fragile nature of juvenile skulls (which are easier to open). But the association indicated between opening of crania and eagle breeding (Chapter 6) suggests that this habit in itself might indicate food stress (more evidence for this is provided later). Increases in the incidence of both opening of hyrax crania and capture of juvenile hyrax (especially in 1988) suggest that the eagles may have been coping with a decline in their main prey by taking a greater portion of less profitable prey items and reducing wastage of any prey captured. Hyrax colony counts did in fact indicate a significant overall decline in hyrax numbers by about one third between the end of 1987 and the end of 1990; whilst sightings of hyrax from transects walked through the veld indicated that this decline was evident during 1986 and may have reduced the hyrax population by half (Chapters 4 & 5).

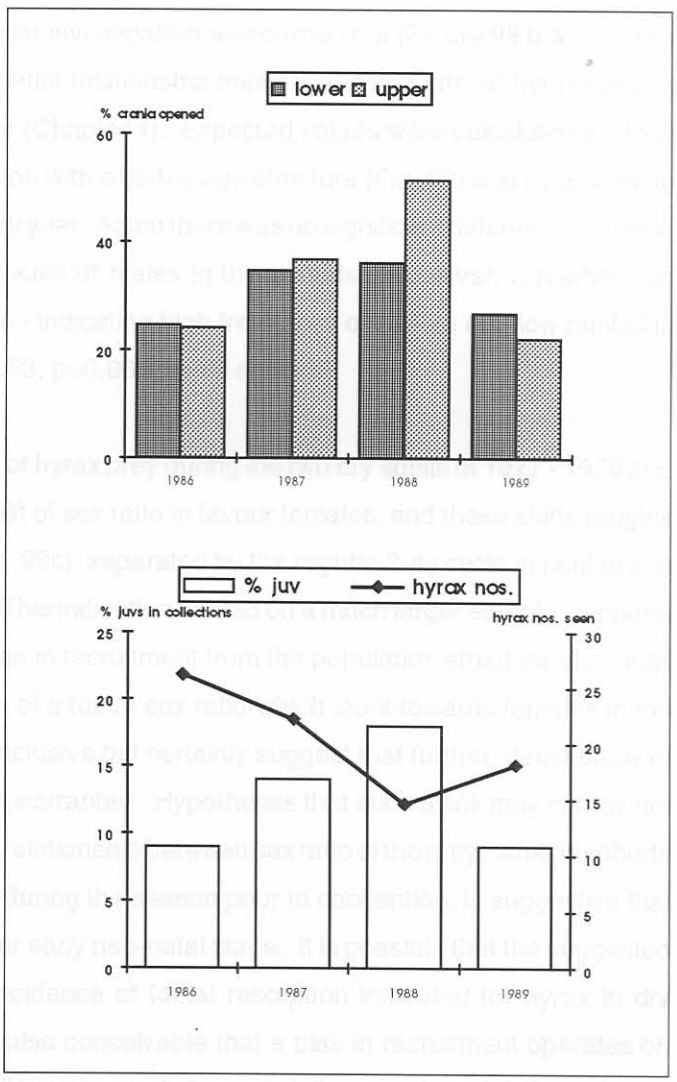



**Figure 98.** Annual change in the percentage of hyrax crania opened by upper and lower escarpment eagles (above), and concurrent change in the juvenile component of hyrax captured (below). Eagles caught more juveniles and opened more crania when colony counts indicated that hyrax numbers were lowest in 1988 (below).

University of Pretoria etd – Davies, R A G (1994)



In order to investigate whether large hyrax birth pulses during wet years led to subsequent high capture frequencies for these cohorts by black eagles, the year of birth was predicted for all fresh skulls collected. Observed frequencies of hyrax captured from each cohort were then compared with expected values had the eagles been preying upon a stable age structure with regular recruitment (as determined earlier in this chapter - see Fig. 92). Observed and expected numbers of hyrax removed from each cohort are plotted in Figure 99a. There was no statistically significant difference between these two distributions overall. However, when residual proportions were calculated for each cohort as: (observed-expected)/expected, these residuals (n=17) showed a significant, positive correlation with rainfall in the previous summer season, prior to conception of the respective cohorts ($r=0,61$; $p<0,01$). This pattern among hyrax prey of black eagles confirm that the prey population age structure is indeed influenced by relayed effects of variable recruitment, as observed by Fourie (1983) and in the present study (Chapter 4).

Prompted by the observation that high predominance of males amongst immature hyrax captured during 1986 and 1987 did not persist beyond that (Figure 96), a similar investigation was carried out (Figure 99 b & c) to see whether the hyrax prey of black eagles reflected a potential relationship between the sex ratio of hyrax cohorts and rainfall at the time of their birth as suggested earlier (Chapter 4). Expected values were calculated as if the eagles were continually capturing hyrax from a population with a stable age structure (Fig. 92) and by assuming that equal numbers of males and females were born every year. Again there was no significant difference between the overall patterns of observed and expected frequencies of males in the cohorts. However, a relationship between high values for residuals (calculated as before - indicating high frequency of males) and low rainfall in the summer season of their birth was suggested ($r=-0,53$; $p=0,066$; $n=13$ cohorts).

There appeared to be a build-up in the male component of hyrax prey during the two dry spells of 1977 - 1979 and 1983 - 1984 (Fig. 99b). Both culminated in a sudden shift of sex ratio to favour females, and these shifts roughly coincided with peaks in the summer rainfall pattern (Fig. 99c), separated by the regular 3-4y cycle in rainfall that is characteristic of the Beaufort West area (Chapter 2). This indication, based on a much larger sample, supports previous statistical evidence of a rainfall-related sex-bias in recruitment from the population structure of a small sample of shot hyrax (page 51), and direct observation of a foetal sex ratio which leant towards females in the wet year of 1989 (page 52). These data are not yet conclusive but certainly suggest that further, direct study of this aspect of hyrax population biology in arid regions is warranted. Hypotheses that such a link may or may not be adaptive were discussed on page 62. The suggested relationship between sex ratio of the prey remains cohorts and rainfall during the season of their birth, rather than during the season prior to conception, is suggestive that any sex-bias in recruitment occurs at the late pre-natal or early neo-natal stage. It is possible that the suggested sex-biased recruitment might be linked with a high incidence of foetal resorption indicated for hyrax in dry conditions (Chapter 4; Millar 1971; Fourie 1983). It is also conceivable that a bias in recruitment operates on immature animals if the filter of predation that acts on dispersing male hyrax is influenced by rainfall one or two years previously, but there were no indications to support this idea.

University of Pretoria etd – Davies, R A G (1994)



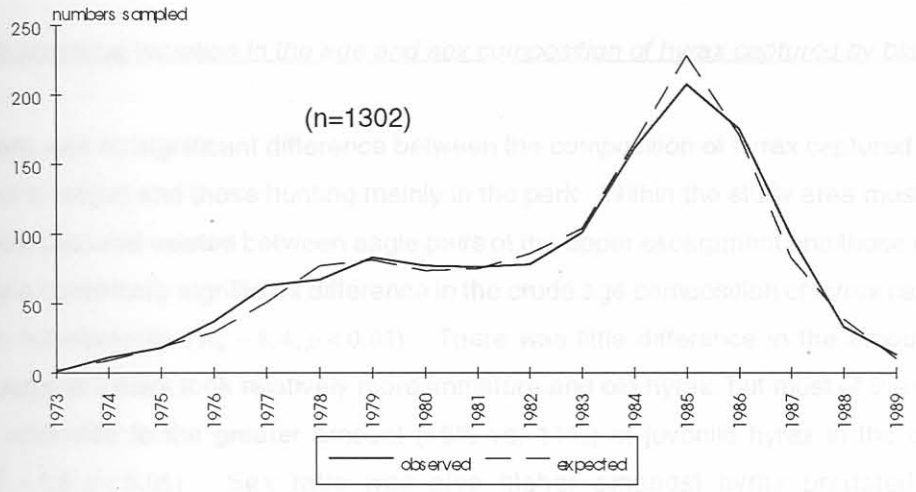



**Fig. 99a.** The birth dates of all hyrax represented by fresh skulls/maxillae in the prey remains were estimated to plot these observed frequencies of cohorts born between 1973 and 1989, among black eagle prey. Expected frequencies were calculated for each cohort as if the eagles had been predating a stable hyrax population with constant rates of recruitment and mortality.

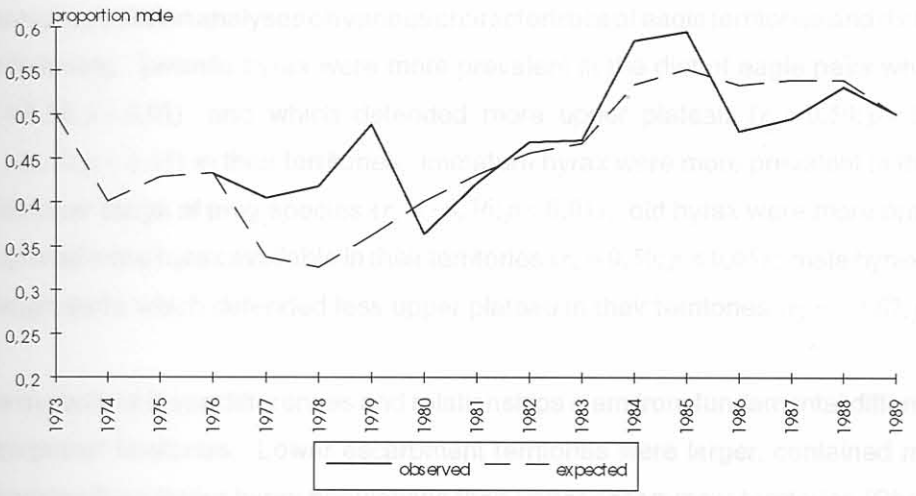



**Fig. 99b.** Observed and expected contribution of males to hyrax cohorts. Observed values were determined from all fresh skulls/maxillae in the prey remains collections. Expected values were calculated for eagles predating a stable hyrax population with a constant and equal production of male and female juveniles each birth pulse.

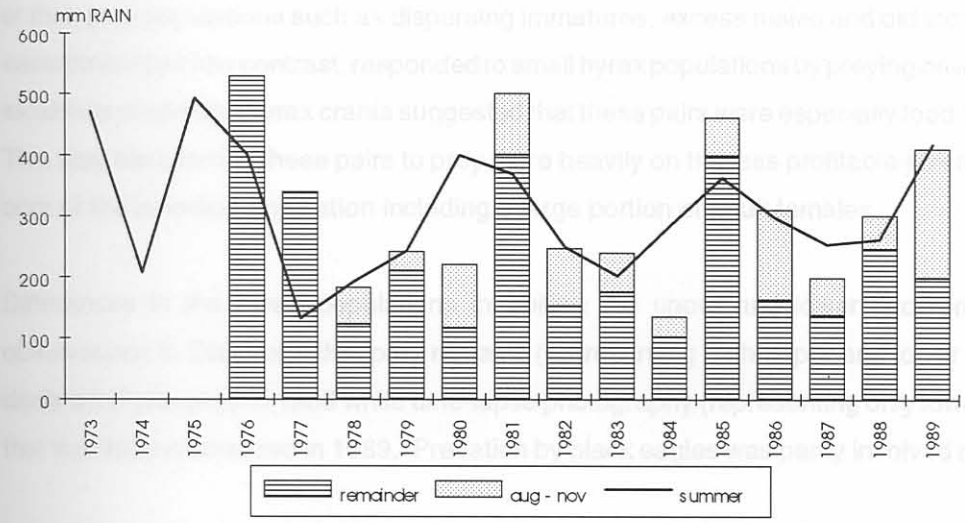



**Fig. 99c.** Rainfall patterns over the years in which the hyrax cohorts represented in the prey remains were born. January to December rainfall is represented as columns (rainfall during late hyrax gestation is lightly shaded); July to June rainfall is plotted as a line.

University of Pretoria etd – Davies, R A G (1994)



*Geographical variation in the age and sex composition of hyrax captured by black eagles within the study area*

There was no significant difference between the composition of hyrax captured by black eagles hunting mainly over farmland and those hunting mainly in the park. Within the study area most variation in the composition of hyrax captured existed between eagle pairs of the upper escarpment and those of the lower escarpment. There was a statistically significant difference in the crude age composition of hyrax captured by eagles nesting on the two escarpments $(K_3^2 = 8,4; p < 0,01)$. There was little difference in the amounts of adult hyrax killed; lower escarpment pairs took relatively more immature and old hyrax; but most of the difference in composition could be attributed to the greater amount (15% vs. 11%) of juvenile hyrax in the diet of upper escarpment pairs $(K_1^2 = 5,6; p < 0,05)$. Sex ratio was also higher amongst hyrax predated by upper escarpment pairs $(\bar{x} = 1,53\ females/male)$, than amongst those predated by lower escarpment pairs $(\bar{x} = 0,98\ females/male)$. This difference was statistically significant $(K_1^2 = 4,5; p < 0,05)$.

General correlation analyses on various characteristics of eagle territories and diet of the respective pairs revealed the following: juvenile hyrax were more prevalent in the diet of eagle pairs which took a wider prey spectrum $(r_p = 0,58; p < 0,01)$, and which defended more upper plateau $(r_p = 0,59; p < 0,01)$ and less middle plateau $(r_p = 0,50; p < 0,05)$ in their territories; immature hyrax were more prevalent in the diet of eagle pairs which took a narrower range of prey species $(r_p = -0,76; p < 0,01)$; old hyrax were more prevalent in the diet of eagle pairs which had more hyrax available in their territories $(r_p = 0,50; p < 0,05)$; male hyrax were more prevalent in the diet of eagle pairs which defended less upper plateau in their territories $(r_p = -0,67; p < 0,01)$.

The majority of these differences and relationships stem from fundamental differences between lower and upper escarpment territories. Lower escarpment territories were larger, contained more mountain slopes and thus accommodated larger hyrax populations than upper escarpment territories (Chapter 6). Eagle pairs nesting on the lower escarpment took a greater portion of hyrax in their diet (Chapter 9). It is likely that these pairs were less hard-pressed to capture hyrax and accordingly could prey on the more vulnerable and superfluous components of their prey populations such as dispersing immatures, excess males and old individuals in senescence. Upper escarpment pairs by contrast, responded to small hyrax populations by preying on a wider species spectrum. High incidence of opening hyrax crania suggested that these pairs were especially food-stressed during 1988 (Fig. 98). This may have forced these pairs to prey more heavily on the less profitable juvenile age class, and on the main core of the breeding population including a large portion of adult females.

Differences in the hyrax populations inhabiting the upper and lower escarpments might also explain the observations in Chapter 9 that prey remains (representing both upper and lower escarpment pairs) indicated a decline in hyrax prey in 1988 while time-lapse photography (representing only lower escarpment pairs) indicated that this decline occurred in 1989. Predation by black eagles was partly involved in these declines (Chapter 12).

University of Pretoria etd – Davies, R A G (1994)



*Regional variation in the age and sex composition of rock hyrax captured by black eagles*

Age and sex-determination of all rock hyrax skulls housed at the S. A. Museum which had been collected by Boshoff *et al.* (1991) from beneath black eagle eyries in the Cape Province, permitted investigation of wide-scale geographic variation. Population structure diagrams for rock hyrax remains collected in seven principal regions of the Cape Province are presented in Figure 100. For two of these regions, population structure could be contrasted for collections made in the early 1970's and in the late 1980's. Data on rock hyrax captured by black eagles in the Mountain Zebra National Park in the early 1980's were accessed from Fourie (1983).

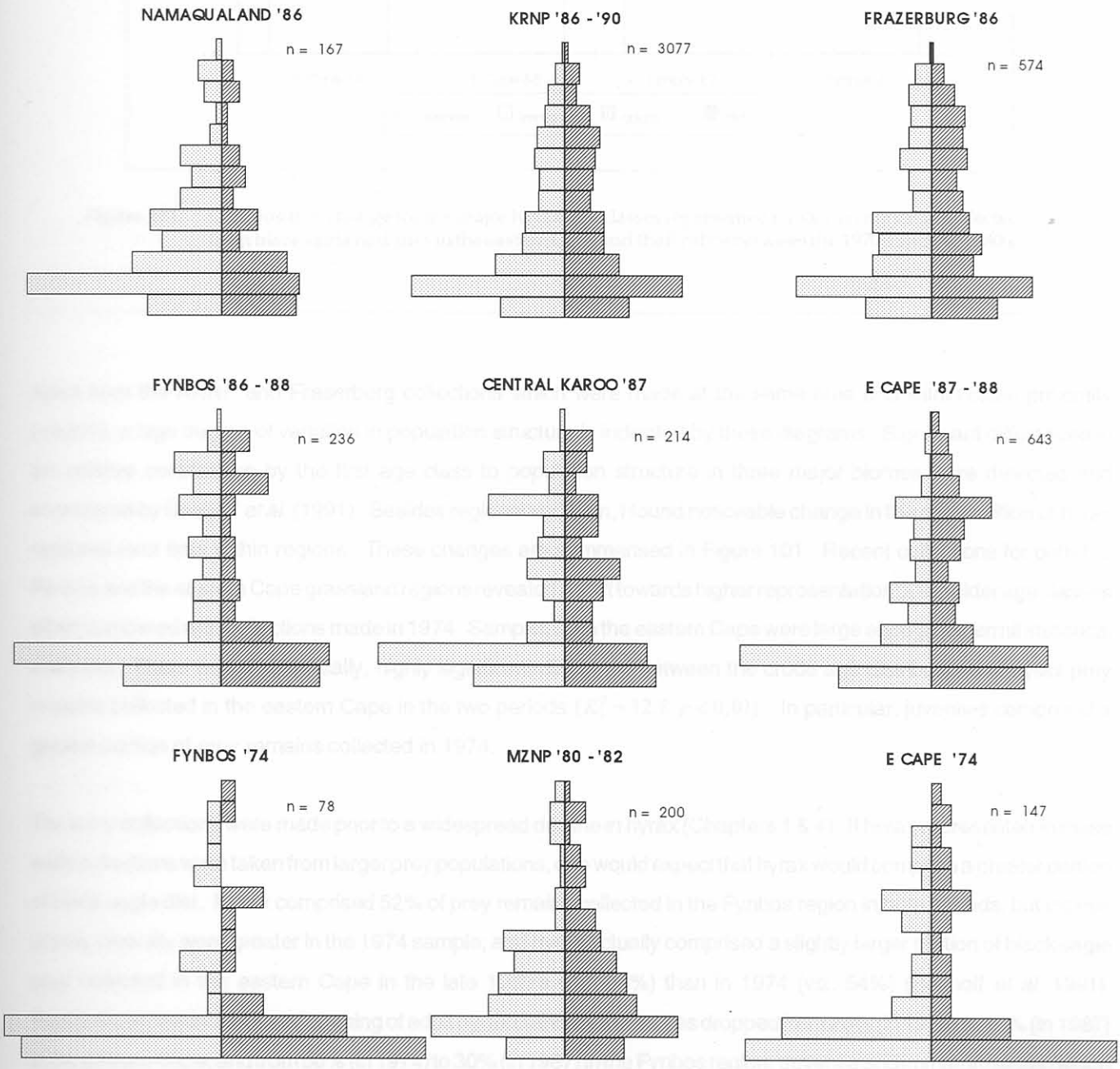



**Figure 100.** Population structure diagrams derived from hyrax skulls/maxillae collected beneath black eagle nesting sites for Namaqualand, the eastern Cape, Fynbos and four areas of the Karoo during the 1980's; and for the eastern Cape and Fynbos during the 1970's. These diagrams were determined from material collected by Boshoff et al. (1991), except for the KRNP (present study) and the MZNP (referenced from Fourie 1983). Males are shown to the left of the axes, females to the right; juvenile age classes at the base-line. Sample sizes are provided.

University of Pretoria etd – Davies, R A G (1994)



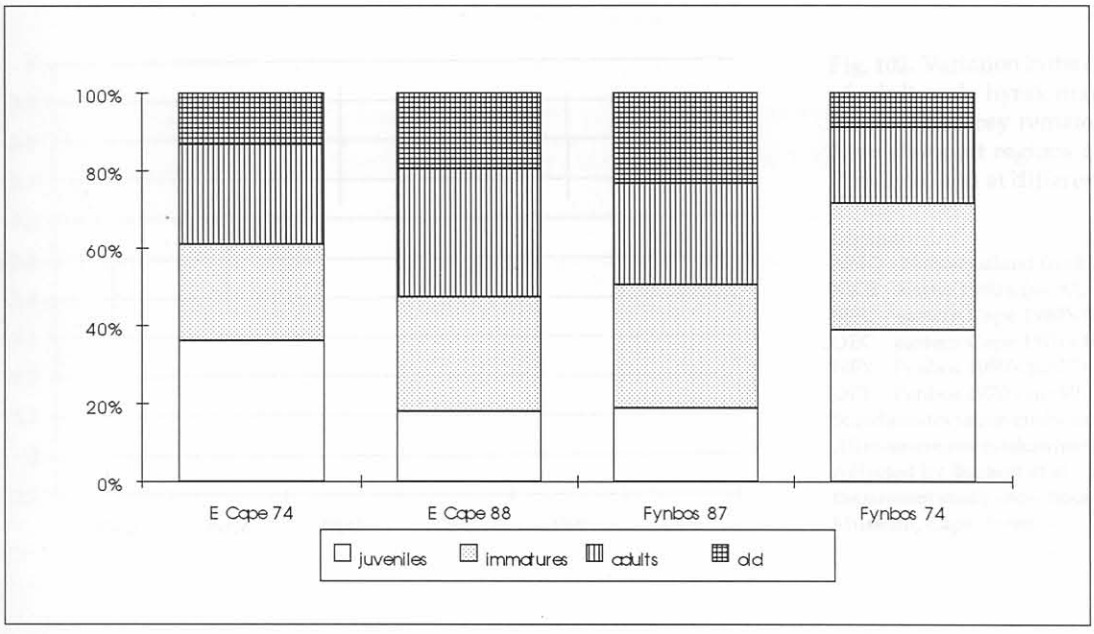



**Figure 101.** Composition change for the major hyrax age classes represented by skulls/maxillae collected from black eagle nest sites in the eastern Cape and the Fynbos between the 1970's and the 1980's.

Apart from the KRNP and Fraserberg collections which were made at the same time and within close proximity (<80km), a high degree of variation in population structure is indicated by these diagrams. Significant differences in the relative contribution by the first age class to population structure in three major biomes were detected and considered by Boshoff *et al.* (1991). Besides regional variation, I found noticeable change in the composition of hyrax captured over time within regions. These changes are summarised in Figure 101. Recent collections for both the Fynbos and the eastern Cape grassland regions revealed a shift towards higher representation of the older age classes when compared with collections made in 1974. Samples from the eastern Cape were large enough to permit statistical analyses. There was a statistically, highly significant difference between the crude age distributions of hyrax prey remains collected in the eastern Cape in the two periods ($K_3^2 = 12,8; p < 0,01$). In particular, juveniles comprised a greater portion of prey remains collected in 1974.

The early collections were made prior to a widespread decline in hyrax (Chapters 1 & 4). If hyrax represented in these early collections were taken from larger prey populations, one would expect that hyrax would comprise a greater portion of black eagle diet. Hyrax comprised 52% of prey remains collected in the Fynbos region in both periods, but indices of prey diversity were greater in the 1974 sample; and hyrax actually comprised a slightly larger portion of black eagle prey collected in the eastern Cape in the late 1980's (viz. 64%) than in 1974 (viz. 54%) (Boshoff *et al.* 1991). Furthermore, the incidence of opening of adult hyrax crania by the eagles dropped from 20% (in 1974) to 15% (in 1987) in the eastern Cape; and from 50% (in 1974) to 30% (in 1987) in the Fynbos region. Juvenile and immature skulls (which are easier to open) were excluded from this analysis, so it appears that the eagles may have been more food-stressed up until 1974.

University of Pretoria etd – Davies, R A G (1994)



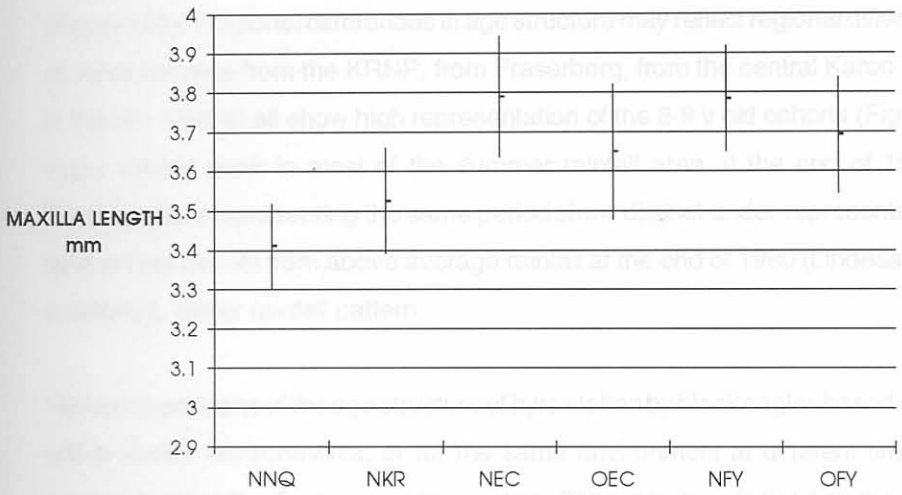



**Fig. 102.** Variation in the size (length) of adult male hyrax maxillae from black eagle prey remains collected from different regions of the Cape Province, and at different times.

Legend:
NNQ - Namaqualand (n=41);
NKR - Karoo 1980's (n=50);
NEC - eastern Cape 1980's (n=50);
OEC - eastern Cape 1970's (n=50);
NFY - Fynbos 1980's (n=37);
OFY - Fynbos 1970's (n=10).
Standard deviation on the mean is shown. All measurements taken from hyrax skulls collected by Boshoff *et al.* (1991), and in the present study - now housed at the S.A. Museum, Cape Town.

Low representation of adult and old hyrax age classes from the early collections in both regions corresponds to a period of drought in the summer rainfall area of southern Africa during the 1960's at the time of birth of those cohorts (Tyson 1986 - Fig 1.11). Whereas high representation of older age classes in the late 1980's collections corresponds to good rains during the late 1970's. It appears that the 1960's drought may have caused reduced recruitment of hyrax cohorts and also reduced individual growth. Skull dimensions of adult male hyrax were larger for the 1987 collections than for the 1974 collections in both regions (Figure 102), although this difference was only significant for the larger samples of adult males collected in the eastern Cape (for length of maxillae: t=3,41; p<0,01; for width of maxillae: t=4,1; p<0,01). From scaling, linear differences suggest that the mass of rock hyrax could have been 12,5% and 6,5% larger for the recent collections in the eastern Cape and Fynbos respectively.

It has been suggested that body mass in *P. capensis* is related to temperature (Yom Tov in press) or perhaps vegetation type (R.G. Klein *in litt.*). The present observations indicate that body mass in rock hyrax maybe more closely related to precipitation and consequent food availability. From scaling, linear differences (Figure 102) indicated that mean hyrax mass in the very dry Namaqualand might be 12% less than mean hyrax mass in the Karoo (2040g: Chapter 4); and that mean hyrax mass in the wetter eastern Cape and Fynbos regions might be >20% larger than mean hyrax mass in the Karoo. The variation in the linear dimensions of adult male hyrax skulls was certainly significant across the various regions ($F_{3,174} = 86,9; p < 0,01$).

Differences in the age structure of hyrax captured during the two decades suggest that the prey population was in different stages of growth at those times. The high representation of younger animals in the 1974 collections suggest that the eagles were preying on less accessible prey populations (smaller?) which were possibly growing. The high representation of older animals and reduced evidence of food stress in the late 1980's collections suggest that the eagles were preying on more available prey populations (larger?) which may have been declining. The degree of representation of cohorts in other regions and at other times can also be explained in terms of the expected effects of rainfall on recruitment and growth of the population. The sudden increase in representation of cohorts younger than

University of Pretoria etd – Davies, R A G (1994)


6 y in the MZNP collection (Fourie 1983) also suggests that this population began increasing in earnest from 1974 on (Figure 100). Regional differences in age structure may reflect regional differences in rainfall. For instance collections of hyrax remains from the KRNP, from Fraserberg, from the central Karoo and from the eastern Cape (all collected in the late 1980's) all show high representation of the 8-9 y old cohorts (Figure 100) which probably correspond to a major rainfall peak in most of the summer rainfall area at the end of 1980 (Lindesay 1984). Collections from Namaqualand representing the same period show distinct under-representation of the 8-10y old cohorts. Namaqualand did not benefit from above average rainfall at the end of 1980 (Lindesay 1984). The Fynbos region is subject to a different, winter rainfall pattern.

While comparisons of the age structure of hyrax taken by black eagles based on tooth eruption and wear are acceptable within similar environments, or for the same environment at different times, comparisons across widely-differing regions such as the Fynbos and the eastern Cape may be criticised on the grounds that hyrax diet and tooth wear is likely to vary between such regions. Some bias may have been introduced by differential tooth wear but it is considered unlikely that this bias would mask the observed, major differences between the samples. Correlation between the age structure of the various samples and rainfall patterns for the respective regions would appear to indicate that the methods are widely applicable.

The age distributions of hyrax captured by black eagles at different times (Figures 100 & 101) supply good evidence for the notion that hyrax populations showed a widespread increase during the late 1970's and a widespread decline in the early 1980's. This is in keeping with many hearsay reports (Chapters 1 & 4). One might expect a long-term synchrony between growth and decline phases of hyrax populations and the nine year wet and nine year dry cycle observed by Tyson (1986: Fig. 1.11) for the summer rainfall areas of southern Africa. In which case, regular cycles of rock hyrax abundance would be generated by regular climatic effects. Climate is not considered to be the cause of cyclicity for small mammals in the far northern hemisphere (see Chapter 12).

The patterns of variation suggest that most of the differences in composition of hyrax taken by black eagles might be explained in terms of differences in the availability of the different prey population components. However, predominance of juvenile hyrax in collections of prey remains appears to be a regular feature of eagles which are thought to be preying on smaller hyrax populations and perhaps suffering from food stress. This was evident for comparisons of the upper and lower escarpment territories, and for comparisons of annual collections in the present study where changes in the composition of hyrax captured did not clearly correspond to changes in the relative availability of the population components. The same trend was evident in comparisons of hyrax captured in 1974 and in the late 1980's. Boshoff *et al.* (1991) ascribed the heavy reliance upon juvenile hyrax age classes by fynbos black eagles to growing prey populations. But again, the Fynbos eagles took the least hyrax in their diet (52%) and showed most evidence of food-stress (30-50% adult crania opened). It appears that black eagle diet varies along a continuum from one extreme where they take a large component of hyrax in their diet made up mostly of males and older age classes, to another extreme where they take a wide variety of alternate prey and the smaller hyrax component is made up mostly of younger age classes and females. Heavy predation of breeding females has been associated with predators exerting a strong limiting influence on their prey (Korpimäki 1985b; Sinclair *et al.* 1990).

University of Pretoria etd – Davies, R A G (1994)


A similar variation involving spotted hyenas *Crocuta crocuta* and blue wildebeest *Connochaetes taurinus* was observed by Kruuk (1970, 1972a) in two regions of East Africa: hyenas killed relatively more surplus components (old and weak individuals) from large prey populations in the Serengeti, and relatively more healthy adults from relatively small prey populations in Ngorongoro. It would appear that reliance on surplus elements of mainly one prey population is a luxury enjoyed by predators experiencing a high ratio of prey to predator, such as hyenas inhabiting the Serengeti in Kruuk's studies and the black eagles inhabiting the lower escarpment in the present study. Correlation analyses performed on a database of the prey remains collected at 53 different sites (samples <20 excluded) around the Cape Province revealed that high representation of juvenile hyrax was indeed associated with high prey diversity in diet $(r_p = 0,38; p < 0,01)$, and with an adult sex ratio that favoured females $(r_p = 0,27; p < 0,05)$; whilst high representation of adult age classes was associated with a greater proportion of hyrax in the diet $(r_p = 0,47; p < 0,01)$. There was a slight tendency for the incidence of opening of adult hyrax crania to be high where hyrax proportion in the diet was low, but this could not be demonstrated significantly $(r_p = -0,31; p = 0,08)$.

As suggested earlier, black eagles may be forced to reduce wastage, to prey more heavily on alternate prey species and on the less profitable younger age classes when their main prey is less available (low prey:predator ratio). These dietary traits may be used to indicate the state of availability of hyrax populations in black eagle territories. Hyrax populations may be naturally sparse due to low density of suitable rock outcrops. This is probably the case for the Cape Fold mountains (Fynbos). Large eagle territories in such terrain are likely to support a greater number of alternate prey which are more likely to be encountered by the wide-ranging, hunting eagles. The Nuweveldberg and the Matobo Hills probably represent the other extreme where high hyrax densities permit black eagles to nest very close together (Chapter 6). The smaller territories maintained by these eagles would support fewer alternate prey and these eagles must subsist predominantly on the large hyrax populations. Consequently these eagles should be more susceptible to fluctuations in their hyrax prey base, and this would appear to be borne out by recent rather dramatic changes in black eagle territories in the Matobo Hills (Gargett 1993 unpubl.). Against these constraints on hyrax populations imposed by the nature of the rocky habitats, variation in rainfall and plant production can lead to major long-term changes in the abundance of hyrax which are reflected in the composition of eagle diet.

Most of the variation in the species composition of black eagle diet and in the age and sex composition of hyrax caught by black eagles must be caused by these major influences. The great variability in the age and sex composition of hyrax taken by black eagles evident in Figure 100 must surely be an indication of the dynamic nature of the structure of rock hyrax populations. But on top of these effects it appears that the eagles can alter the emphasis of their selective predation, most notably by taking more juveniles when conditions get hard. In the case of the black eagle-rock hyrax system in the water-limited karoo environment, droughts and rainfall events probably lead to sudden changes in hyrax vulnerability and consequent predation by eagles, perhaps without significant change in absolute hyrax abundance. One would expect that high representation of naive younger age classes in eagle diet would be characteristic of hyrax populations which are well protected within their habitat and are able to grow in the absence of heavy predation pressure; whereas high representation of the more experienced older age classes in eagle diet would be characteristic of hyrax populations which are in great excess to their carrying capacity and are declining. So the degree to which hyrax populations are in balance with their carrying capacity set by the vegetation within the safe confines of the rocky habitat is also likely to be a major influence on the emphasis of age and sex-specific predation by black eagles.

University of Pretoria etd – Davies, R A G (1994)



CHAPTER 11

# LIVESTOCK PREDATION BY BLACK EAGLES IN THE KAROO

## INTRODUCTION

Nearly 9000 years ago the first sheep were domesticated on the steppes surrounding the Aral and Caspian seas (Zeuner 1963). This marked a transition in human foraging behaviour from hunter-gatherers to agriculturalists and pastoralists. With growing technologies, human beings have exercised progressively more control over the resources on which they depend. Domestic sheep have provided a very significant portion of the essential resources of food and clothing. The world population of domestic sheep has been estimated at over 1000 million animals (Squires 1975), and one third of these occur in six southern hemisphere countries. South Africa, being one of these, had an estimated population of 44 million woolled sheep in 1930, but after the boom in the wool industry this declined to about 17 million (Anon 1985). Total sheep and goat numbers in the Karoo are estimated at approximately nine and a half million (Table 41, p. 247).

With domestication, the influence of natural selection has been increasingly replaced by that of selective breeding. While sheep have been bred for efficient production of harvestable commodities, they have become more dependent on humans and progressively less capable at evading natural predators. Many large predators have taken advantage of such easy prey and thereby have come into direct competition with the farmer for this resource. This competition is aggravated further when the vulnerability of sheep elicits a surplus killing response by the predator (Kruuk 1972b; Stuart 1986). Farmers are more inclined to accept sheep losses caused by climate or disease, resignedly. But the violent loss of lambs or ewes to a predator evokes a more angry and defiant response.

The extent of predation on livestock as revealed by questionnaire surveys is often exaggerated by the majority of ranchers who do not carry out thorough investigations of mortality agents (e.g. Nesse, Longhurst & Howard 1976; Armentrout 1980; Boshoff 1980; Hewson 1981). Despite this, there is no doubt that predators can seriously detract from the success of sheep-farming operations under certain circumstances. Coyotes *Canis latrans* caused an estimated U.S.$ 50000 worth of damage to livestock on a western Montana ranch over a 30 month period (O'Gara *et al.* 1983), and led to an estimated 14 - 23% decline in revenue and an estimated 16 - 33% increase in costs on an Angora goat ranch in Texas (Schrivner & Conner 1984). Domestic dogs are also implicated as regular predators of livestock in North America (Schaefer, Andrews & Dinsmore 1981). The estimated value of sheep losses to coyotes and dogs in California was equivalent to 10% of the total income from a ranching enterprise (Schrivner, Howard, Murphy & Hays 1985). In Australia, feral pigs *Sus scrofa* (Moule 1954) and 'killer' foxes *Vulpes vulpes* (McDonald 1966) have caused extensive damage. In Scotland foxes are held to be the chief offenders (Lockie 1964; Hewson 1984). While in South Africa caracals, black-backed jackals and domestic dogs are responsible for most sheep depredations (Rowe-Rowe 1975; Roberts 1986; Lawson 1989; Bekker *in litt.*). The only costing of predation in the Karoo was by Siegfried (1963b), who estimated the damage caused to sheep in the Great Karoo by corvids at R10860 p.a..

University of Pretoria etd – Davies, R A G (1994)



Wildlife biologists point out that losses to predators often only account for a few percent of the flock each year. But when these proportions are applied to nationwide flock sizes under the questionable assumption of non-compensatory predation (i.e. all stock would have survived to market had they not been killed by predators), it is easy to see why the early wildlife managers introduced bounty systems on 'problem' animals in the vain hope that losses might be prevented through elimination of all non-human predation. The U.S. Fish and Wildlife Service (1978) calculated that sheep losses to predators over 17 western States in 1977 were worth between 19 and 38 million dollars. In Texas alone, small stock losses to predators were valued at U.S.$ 13 million during 1978 (Texas Crop & Livestock Reporting Service 1979). Lawson (1989) valued the annual toll of sheep taken by predators in Natal at three million Rands.

Bounty systems have been used in attempts to eradicate predators from all the major sheep-farming regions of the world, and have encouraged enormous efforts and sometimes expenses on the part of the ranchers and trappers. The bounty system proved very popular in the Cape Province, South Africa, earlier this century. It is estimated that 120000 caracals were destroyed for the bounty system between 1931 and 1981, and in a single year (1949) 656826 bounties were paid out for predators destroyed (Stuart 1987a). The main methods of control in the Cape were shooting, gin traps, poisons and the formation of hunt clubs using dogs (cage traps, coyote getters, toxic collars and 'humane' killer traps have been used more recently). In addition, jackal-proof fencing of Cape farms was completed by about 1920 at great expense. The cost of erecting just the 7600km of road-side jackal-proof fencing in the Cape Province was recently estimated to be nearly R23 million (Siegfried *in litt.*).

In the case of large predators such as lions *Panthera leo*, spotted hyenas, and cheetahs *Acinonyx jubatus* which are arguably incompatible with sheep-farming, this effort has been successful in the Cape Province (Stuart, MacDonald & Mills 1985). But smaller predators such as black-backed jackals and caracals which pose less threat on an individual basis and which are probably more difficult to eradicate, still persist in large numbers. Eradication of black-backed jackals has been partly successful in the Great Karoo below the continental escarpment. Norton (*in litt.*) provided bounty records from the Cape Provincial Administration which show that a gradual decline in the kill rate of black-backed jackals in the Karoo has been concurrent with a steady increase in the kill rate of caracals. The records reveal that in the Beaufort West district 728 jackals (this figure probably includes foxes) and only 2 caracals were killed during the 15 years preceding 1947, compared with a kill of 37 black-backed jackals, 825 Cape foxes, and 75 caracals in the eight years thereafter. They also indicate a gradual increase in caracal kill rates for the Fynbos, coastal and eastern Cape regions. This predator has now become the principal 'problem animal' in the Cape (Stuart 1987b). Caracals predominate in the rocky mountainous regions, and the inaccessibility of such broken terrain is often associated with heavier livestock depredations (e.g. Nass, Lynch & Theade 1984).

The discovery that the expensive bounty systems were largely ineffective at reducing the numbers of such predators (Connolly 1978; Stuart 1982), coupled with a change in conservation attitude led to their discontinuation in the Cape (Hey 1959) and other parts of the world. But the State paid out a subsidy of R58690 to hunt clubs in 1985/86 (Siegfried *in litt.*) and control measures are still actively employed by individual farmers and the problem animal control section of the Cape Nature Conservation Department. On one farm in rocky terrain near Victoria West, 141 caracals and 6 black-backed jackals were destroyed between 1978 and 1990 (records for other predators killed were only

maintained from 1978 to 1980 when 24 Cape wildcat, 9 Cape fox and 1 aardwolf were destroyed - Swiegers *in litt.*). It was a visit to this farm in 1984 and the observation of hyrax and other prey epidemics that prompted the present study (Chapter 1). Many farmers such as this spend a lot of time and resources on predator control without any indication that their caracal 'problem' is declining. Sadly, an enormous amount of non-target species are being killed in this process because of non-selective methods, notably poison and gin traps (Brown 1988a; Allan 1989). Furthermore, the expense of some predator control operations has been shown to actually exceed the value of the animals that are lost to predators (Schrivner & Conner 1984), and a new notion is that small improvements in flock management may have far more beneficial effect on harvests than large efforts to control predators (Hewson 1984; C.J. Brown pers. comm.).

Large eagles were not exempt from bounty systems, and have been persecuted wherever they occur in major sheep-farming regions (Brown 1975). An estimated 20000 golden eagles were shot from light aircraft in the states of Texas and New Mexico between 1942 and 1962, while 700 wintering eagles were shot by helicopter in Wyoming over one season (Spofford 1964, 1975). Single hunters boasted kill rates as high as 1200 eagles in a season, and 12000 over 20 years (Johnstone 1966). Unlike coyote and caracal populations, large eagles have a low potential for population increase (Brown 1976; Newton 1979) and such heavy persecution has undoubtedly been a major factor in the decline of many eagle populations around the world. Kill rates of wedge-tailed eagles in Australia were considered to be the highest for any large raptor (Brown, L.H. 1976: p. 195). It was estimated that the total eagle kill in Australia may have exceeded 30000 per annum (Serventy 1974). This persecution probably reduced eagle populations in the more unstable, arid areas (Ridpath & Brooker 1986). But these kill rates were far lower than those claimed by farmers for black and martial eagles in parts of the Karoo during the 1960's (Siegfried 1963a; Chapter 1: p. 3). Approximately 5000 eagles were destroyed in the Cape Province between 1935 and 1950 for the bounty system (Boshoff & Vernon 1980), and as many as 520 bounties were paid for dead eagles in one year (Stuart 1987b).

Since the bounty system was withdrawn in the Cape there has been a major, sympathetic shift in the attitudes of farmers towards eagles. This has been largely due to education programmes run by the Cape Nature Conservation Division and other organisations (Boshoff 1978, 1980; CDNEC undated). Today, eagles enjoy a greater degree of protection by karoo farmers (Janse van Rensburg 1991), and a generally more popular public image in many parts of the world (Kellert 1985). However, eagles are still being killed unintentionally by farmers in the Cape through the use of non-selective methods of predator control. The widespread and indiscriminate use of poison is considered to be responsible for the disappearance of bateleur eagles and other large scavenging raptors from the Karoo (Pickford, Pickford & Tarboton 1989; Allan 1989) and other small stock farming areas in southern Africa (Brown 1988a, 1991). Meanwhile, direct persecution of eagles continues unabated in certain isolated farming communities such as Merweville (pers. rec.) and Steytlerville (Anon 1992a unpubl.).

Do eagles really compete with farmers by preying on livestock, and is the persecution of eagles at all justified? Black eagles are known to perch boldly on carcasses of dead sheep or lambs which may have been killed by more secretive predators or died non-violently (C.J. Brown pers. comm.), so to what extent is the notion that eagles kill lambs a perceptual problem? It is certainly based on very little documented evidence. However, eagles are powerful avian predators and there are records of at least two species killing young ungulates weighing up to and over 30kg (see

University of Pretoria etd – Davies, R A G (1994)


Table 26, p. 178). Although exceptional, the records in Table 26 do indicate that the larger eagles should be capable of overpowering young sheep up to about half size. To many farmers this may be justification enough for getting rid of them. But on the basis of very few documented observations and some hearsay accounts, the issue appears to be not whether eagles kill lambs, but rather to what extent does lamb-killing by eagles occur, and under what circumstances?

Most studies and hearsay accounts indicate that only very young lambs (up to about 10d old) are susceptible to eagle predation (Arnold 1954; Wiley & Bolen 1971; Tjernberg 1981; Hewson 1984). Lambs born under open-range conditions (as practised in the Karoo) are most vulnerable to any eagle attacks (Phillips & Blom 1988). There is also evidence that younger, less experienced (non-breeding) eagles are more inclined to kill lambs (Foster & Crisler 1978). One instance of eagles causing extensive damage to small stock farming involved an aggregation of predominantly juvenile golden eagles in Montana following a major decline in the natural prey base. This investigation by O'Gara (1978) suggested that eagle damage on two ranches amounted to U.S.$ 38000 in 1974 and U.S.$ 48000 in 1975. Littauer & White (1981) valued damage to livestock by golden eagles in New Mexico during one lambing season at U.S.$ 87000.

Most studies of eagle-livestock depredations have implicated the golden eagle in North America (e.g. O'Gara 1978; Phillips & Blom 1988) and in Europe (e.g. Weir 1985; Bergo 1987), but bald eagles *Haliaeetus leucocephalus* in America (Wiley & Bolen 1971; McEneaney & Jenkins 1983) and white-tailed sea eagles *Haliaeetus albicilla* in Europe have occasionally been implicated. In Australia the wedge-tailed eagle is known to kill lambs and there are some reports of white-bellied sea eagles *Haliaeetus leucogaster* feeding on domestic stock (Leopold & Wolfe 1970; Rowley 1970; Brooker & Ridpath 1980). Here in Africa the martial, black and crowned eagles (the most rapacious species) may kill lambs (Boshoff 1980; Boshoff *et al.* 1990; Boshoff *et al.* 1991; Bekker *in litt.*), with some indication that the smaller tawny eagle also uses this food resource (Boshoff, Rous & Vernon 1981). Large forest eagles such as the crowned eagle, the harpy eagle *Harpia harpyja* in South America and the Philippine eagle *Pithecophaga jefferyi* may kill livestock, but their ranges do not overlap with major small stock farming regions. New Zealand is the only major sheep-farming region where large eagles do not presently occur (Brown & Amadon 1968).

An objective assessment of the black eagle as a livestock predator in the Karoo was needed. A major, applied motivation for the present study was to assess the 'role' of black eagles on karoo farms, so this chapter is intended as a summary of the harm that they can do on farmland. I have attempted to address the following questions: to what extent and under what circumstances do black eagles kill lambs in the Karoo? how does this predation influence livestock numbers and the revenue from ranching operations? and in the event of livestock predation by black eagles, what management steps are effective and practical for the prevention or reduction of losses? Nest-based studies of eagle feeding habits have serious limitations when used to address these questions, so I rely on other methods such as the collation of farmers' reports and field necropsies on lamb carcasses. The relative brevity of this chapter is due to the extreme difficulty that I experienced in finding any evidence of lamb-killing by black eagles, and the need to focus on the main predator-prey (hyrax) relationship. In consequence, I draw heavily on the literature regarding questionnaire surveys and investigations of lamb predation world-wide, to draw conclusions about the compatibility of large eagles with the open-range farming of small livestock. Some of these observations have been published earlier (Davies 1988).

University of Pretoria etd – Davies, R A G (1994)


# METHODS

Methodology used for nest-based studies of black eagle feeding habits in the present study was described in Chapters 8, 9 & 10. Collections of prey remains from eagle nests give a poor indication of the extent of stock depredations by the eagles because: they only reflect diet during the breeding season; non-breeding birds generally cause more harm; many lambs would be too large to be transported to nests; and most important, they give no indication of whether lambs were scavenged or killed (Matchett & O'Gara 1987). On the other hand, many raptors are known to take a wider spectrum of larger prey items when under strain to feed nestlings, and over-representation of domestic lambs in the diet of the eagles might also be caused if larger skeletal material tends to accumulate in collections of prey remains over time (Chapter 9). The latter bias may be overcome by time-lapse photography and other observations at nests (Chapter 9), but results from these methods are still influenced by the other shortcomings of nest-based methods of diet determination. Direct observations of the eagles within their ranges (Chapter 6) are time-consuming but can yield small amounts of bias-free information on stock predation by territorial birds, or the absence of it. Prolonged observations of eagles in the vicinity of lambing paddocks is probably the best way of getting eye-witness accounts (Brooker & Ridpath 1980), but insufficient time was available for this method in the present study.

Data on stock predation by black eagles were gathered from three other sources: personal interviews with farmers; literature search; and field necropsies of carcasses in the lambing camps. Interviews with karoo farmers were conducted between 1983 and 1990. I delivered several talks to the Beaufort West farming community and asked any farmers to call me out if they were experiencing problems with eagles on their farms. Most visits were restricted to an area within a 250km radius of Beaufort West. I also obtained information on stock predation from casual discussions with members of the farming and conservation communities. A literature search on stock predation was conducted using key-words through 'Dialog Information Services, Inc.' in order to provide data on lamb predation by eagles and other predators around the world. All articles which were readily accessible through libraries were consulted.

Field necropsies were carried out on any lamb carcasses that I came across on visits to farms or during other field work, where an eagle might be implicated as the agent of mortality. The success of these post-mortem examinations depended largely on the state of decay and 'intactness' of the carcasses. The examination involved skinning the carcass and inspecting for characteristic wounds delivered by predators. For eagles, these wounds have been described by a number of authors (Rosko 1948; Rowley 1970; Wiley & Bolen 1971; Alford & Bolen 1972; Bowns, Davenport, Workman, Nielson & Dwyer 1973; Davenport, Bowns & Workman 1973; White 1973; Brown, J.E. 1976; Nesse, Longhurst & Howard 1976; Tigner & Larson 1977, 1981; O'Gara 1978, 1981; Wade & Bowns 1980). Massive subcutaneous haemorrhaging surrounding irregularly-spaced talon punctures on the neck and upper back are the primary indications for eagle-killed lambs. These and other signs of lamb mortality agents were summarised in a short field guide for farmers and conservationists entitled 'Innocent Until Proven Guilty' (published by S A Eagle Insurance Company Ltd., and available through the Endangered Wildlife Trust, Private Bag X11, Parkview 2122, Johannesburg, South Africa).

University of Pretoria etd – Davies, R A G (1994)


## RESULTS AND DISCUSSION

*Nest-based investigations of stock predation by eagles*

The most extensive data on eagle predatory habits derives from collections of prey remains from nest sites. Domestic bovids comprised 1,12% of 3586 prey items collected in and around the Karoo National Park between 1986 and 1990 (Table 28, page 183). All were considered to be immature animals with a mean mass of 4180g (n=40). On account of their relatively large size, domestic bovids fulfilled a slightly larger portion (1,82%) of the eagles' food needs (Table 29, page 185).

Lamb remains were observed relatively more frequently on visits to nests (Table 32, page 189). This is likely to be due to slower consumption of large prey items by the eagles. Lockie (1964) considered that lambs would be over-represented amongst fresh prey remains at golden eagle nests. Analyses of actual prey deliveries monitored by time-lapse photography in the present study did not suggest that domestic lambs were significantly over- or under-represented in collections of prey remains (page 203).

As expected and as revealed in Chapter 9, domestic bovids made up a significantly greater amount of the diet of eagles which hunted predominantly over farmland (viz. 1,6%) than that of eagles which hunted predominantly over parkland (viz. 0,6%). At an average annual predation rate of 174 prey per eagle territory (Chapter 8), this would imply that on mountainous farmland an average of 2,8 lambs would be consumed by eagles per territory (@2300ha) each year, or 5,6 lambs for the average karoo farm (@4687ha: Olivier *in litt.*).

However, underestimation of the lamb component in the present study of black eagle diet may have occurred through some confusion with klipspringer remains (page 202), and because the territories of most eagles nesting on adjoining farmland to the KRNP still encompassed some of the park, from which domestic stock were excluded. In other regions of the Cape Province, black eagles have been recorded to consume more domestic lambs in their diet. Further down the Nuweveld escarpment towards Fraserburg, domestic bovids made up 3,9% of black eagle diet (Boshoff *et al.* 1991). This consumption rate should be free of the influence of conservation areas and would correspond to a consumption rate of up to 6,7 lambs per eagle territory and up to 13,6 lambs per farm in the mountainous parts of the Karoo each year.

East of the Karoo the short shrublands are replaced by eastern Cape grasslands and thick bush. Here black eagles may take up to 8% domestic bovids in their diet (Boshoff *et al.* 1991). Martial eagles were also found to feed on more domestic stock in this region (Boshoff *et al.* 1990). This may be a convergent situation to that observed by Bolen (1975) in Texas, where golden eagles were found to take more domestic lambs in areas of thicker brush. These areas actually contained more natural prey (lagomorphs), so Bolen attributed the higher incidence of stock predation by both eagles and carnivores in the brushlands to the relative inaccessibility of natural prey in this dense vegetation. Wade (1982) also reported high losses to predation among isolated goat populations in thick Texas brush.

University of Pretoria etd – Davies, R A G (1994)



Brown (1975) estimated that between lambing and weaning, 500 - 700 domestic lambs lie dead in the average golden eagle territory in Scotland, and stressed that the eagles do not need to kill lambs in the presence of this food glut. It is estimated that about 145 lambs die on the average karoo farm each year (Table 41, p. 247), and most of these would be available as carrion within two weeks of the lamb births. One would expect an annual mortality of about 70 lambs within the average black eagle territory on farmland. Earlier breeding by farm-nesting eagles suggests that the birds are indeed taking advantage of the food resource resulting from the main lambing period in March in the Beaufort West district (Chapter 6).

While black eagles were twice observed to scavenge on domestic sheep, actual predation was neither observed nor inferred in the present study (see later). It thus seems highly likely that a significant proportion of the domestic lambs conveyed to black eagle nests were scavenged rather than killed by the eagles. Two studies at scottish golden eagle nests provide data on this aspect of eagle feeding habits - signs of predation rather than scavenging were evident on three of ten assayable lamb carcasses delivered to one nest (Lockie 1964) and on two to four of six assayable lambs delivered to another (Weir 1985). This suggests that about 40% of lambs consumed by scottish golden eagles may actually have been killed by the eagles, but the sample is very limited. Most of the various biases inherent in analyses of prey remains mean that this method should yield a worst-case scenario or an upper limit to the maximum levels of stock predation by resident eagles (Methods). One might conclude that the real predation rate of resident eagles would fall well below these indications of their consumption rate of domestic lambs. It is not possible to gauge the exact extent of this predation from collections of prey remains. Furthermore, golden eagle studies (in Matchett & O'Gara 1987) indicate that wandering, food-stressed immature eagles are more responsible for lamb-killing than resident breeding pairs of eagles who might enjoy a more reliable natural prey base. To truly be free of such biases, one must depart from the nest-based food studies and consider the other methods pertaining to the actual lambing paddocks.

*Direct observations*

In the course of fieldwork I did not observe any attacks by black eagles on domestic stock, but I saw eagles scavenging on sheep carcasses twice. In one instance (3/6/87), an adult eagle was flushed from a carcass of a Merino lamb which had recently been killed by a small carnivore immediately south of the Karoo National Park (see field necropsies). On 2 January 1988 I watched an adult pair of black eagles descend from their nest cliffs and alight on the slopes below to feed off the carcass of an adult sheep on the farm Lemoenfontein, Beaufort West.

Direct observations of eagles in the vicinities of lambing paddocks were not conducted in the present study. However in 1983 and 1984, as part of another study, I was conducting observations on springbok and Merino sheep on the farm Biesjiesfontein near Victoria West and had the opportunity of observing eagle behaviour in the presence of lambs of both species. On one occasion, a single adult black eagle was seen to alight on the back of an old and sickly springbok ram, but the eagle flew off when the ram bolted. The remaining observations were of an immature martial eagle which frequented the camp in which I was conducting observations. This young bird may have fledged from a nest in the same camp. Although not the species under study, it shows a similar degree of rapaciousness to the black eagle and I think that the observations are pertinent here.

University of Pretoria etd – Davies, R A G (1994)



Over a period of a few months, I witnessed several attacks by this martial eagle at prey. A young springbok (estimated to be two thirds adult mass) escaped one attack by sprinting up a steep slope; a small springbok lamb and a young bat-eared fox (three quarters adult mass) both escaped the eagle through intervention by nearby adults of their own species (probably parents); an adult suricate was the only kill directly observed; but on another occasion the young martial was flushed from a freshly-killed and mostly-consumed springbok lamb. Throughout this period there were young Merino lambs in the study camp which were probably more vulnerable to attack than any of the natural prey. These lambs occasionally bedded directly beneath a tree which was regularly used as a perch by the eagle. Not once was the eagle seen to attack any of these lambs or to feed on the lamb carcasses that were available.

Young raptors often attack very large prey (Mueller & Berger 1970; pers. obs.) and learn through experience to choose the right prey size. The observed attack on an immature springbok may have been of this nature, which makes it all the more surprising that this young eagle did not attack the Merino lambs. Bird behaviour is often highly influenced by early experiences during sensitive developmental stages. Acceptance of parents or surrogate parents by young birds during their first couple of weeks as nestlings dictates future acceptance of sexual mates when they reach maturity. This process, called 'imprinting', is very different from normal associative learning (Lorenz 1935, 1937; Hess 1973) and can be very difficult to reverse or change (Jones 1981). Besides parents and mates, young birds and other animals have also been shown to imprint on nesting habitat (Klopfer 1963), and on food types (Rabinowitch 1968, 1969; Hess 1973; Meyer-Holzapfel in Lorenz 1973; Immelmann 1975). These strong food preferences can be very persistent (Rabinowitch 1969) and may remain manifest even after a change in diet (Burghardt & Hess 1966). Hess (1973) considers that modification of innate feeding behaviour in domestic chicks during the sensitive period is "apparently permanent". Falconers are well acquainted with the great partiality that trained hawks develop for particular prey species, and describe this affinity as 'wedding' to a particular prey (Woodford 1966). It may take several days of food-deprivation before captive raptors will switch from a diet of white mice to one of day-old chicks (pers. obs.). I think it is highly likely that the young martial eagle under observation was fed natural prey items as a nestling and consequently became wedded or imprinted on these prey types. As a result it simply did not recognise the Merino lambs as potential prey.

Most of the large African eagles will kill newly-born antelope, especially when left unattended (e.g. Mooring 1993). Martial eagles attack lambs of the smaller antelope species even in the presence of their dams, as recorded photographically by Scott (1985: p. 33) and Kunkel (1992). Many of the farmers interviewed in the present study considered that eagles preferred to attack goat kids rather than sheep lambs. Goats often suffer heavier predation than sheep (Nass *et al.* 1984; Wade 1982). Mortality rates for Boer goat kids in the Karoo were indeed higher than those of Merino and Dorper lambs (Roux *et al.* 1981). Greater incidence of goat kid predation by eagles may be due to their closer resemblance to juvenile antelope, but could also be due to poorer attendance by nannies (Glover & Heugly 1970) and to the isolation of goat herds in thick brush and rough terrain (Nass *et al.* 1984).

The favouring of a common prey type by foraging birds has been explained by Tinbergen (1960) who maintains that the birds form a 'specific search image' for that prey type. Specialised predators such as black eagles might be expected to have a very strong 'search image' for their preferred prey, and be even less inclined to switch to a new prey type. This might explain why black eagles are notoriously difficult to trap (Gargett 1990; the present study).

University of Pretoria etd – Davies, R A G (1994)


*Attitudes of farmers to eagles*

During the course of fieldwork, I interviewed over 30 farmers and 11 members of the conservation community with regard to problem animals, particularly eagles. In addition to these casual interviews, I made 29 visits to farms in the Beaufort West, Victoria West, Murraysburg, Hopetown, Kimberley, Swartberg, Graaff Reinet, Fraserberg, Craddock, Tankwa Karoo and Middleberg districts of the Karoo.

Six farmers provided details on eagles that they claimed to have killed. Many farmers maintained that eagle problems became more manifest during drought conditions when natural prey might be in decline. Farmers in the Camdeboo area near Graaff Reinet took action against eagle problems during the 1983 drought: one killed three black eagles and two martial eagles; another killed three black eagles; and a third claimed to have killed nine black eagles in the same locality over a two-week period. Merweville farmers claimed extremely high kill rates of eagles during the 1980's: one claimed that he killed 26 eagles in a single year, and that he had removed a total of 86 eagles from his farm; his neighbour claimed he killed 51 eagles in a single year; another farmer in the area admitted to removing a pair of martial eagles. Most of these birds were captured in gin traps or shot. Other mortalities for black eagles (post-fledging) that I heard of were one electrocution, two drownings in farm reservoirs and one collision with a communications tower. A single poisoning incident did not prove fatal. Trapping, poisoning and shooting are the major causes of mortality in North American golden eagles (Bortolotti 1984) and Australian wedge-tailed eagles (Ridpath & Brooker 1986).

Laingsburg farmers who returned questionnaires in 1963 claimed kill rates which were equivalent to 166 eagles killed per 10000km$^2$ per year (Siegfried 1963a). Most of these were black eagles, and the reported number of this species destroyed was equivalent to nearly twice the expected annual production of black eagle chicks in the district (p. 3). This kill rate is more than nine times that of wedge-tailed eagles in Australia (Ridpath & Brooker 1986), supposedly the most persecuted large raptor in the world (Brown 1975). It became evident during the present study that despite changing attitudes towards eagle conservation, intense persecution of the birds continues in some localities. Most recently, two farmers from Steytlerville claimed to have killed 140 black eagles on their farms over a two year period (Anon 1992a unpubl.). It is not possible to know how accurate these claims of eagle-killing by farmers are. It seems highly unlikely that a single farmer would actually be able to kill 51 eagles on his farm in a single year. Some of these claims may be gross exaggerations to impress peers, or to upset eagle biologists! There is no indication that black eagles are declining in the Karoo, and the population just along the escarpment through the Karoo and into the eastern Cape may exceed 1300 birds (Chapter 6). If these claims of eagle persecution are accurate, then alarming as they seem, they indicate a healthy floating population of non-breeding birds which quickly fill vacant territories. Extremely intense persecution of black eagles in districts such as Laingsburg in the past may have caused these districts to act as 'sinks' for the Cape population. But today eagle persecution, like that of caracals, appears ineffective at controlling predator numbers.

Only 0,6% of 14761 Cape farmers interviewed by questionnaire admitted to persecuting raptors, perhaps in fear of legal action (Boshoff 1980). Information on the beneficial effects of raptors was volunteered by 3,7% of the same farmers. Of all the farmers interviewed in the present study, only two took active steps to encourage eagles on their

University of Pretoria etd – Davies, R A G (1994)



farms (by provision of artificial nest sites, and rehabilitation of injured birds). However many of the farmers, especially around Beaufort West, were prepared to protect their nesting eagles. Some of the farmers who persecuted carnivores intensely (even yellow mongooses *Cynictis penicillata* in one instance) were inclined to tolerate resident eagles. When I visited these farmers, they would often refer to information pamphlets on raptors which had been sent to them by the Cape Department of Nature and Environmental Conservation.

*Farmers' reports of stock losses to eagles*

Of 37 farmers interviewed, 18 (49%) reported that they had suffered no domestic stock losses to eagles. One of these farmers however reported that he often lost springbok lambs to a resident pair of black eagles. A search at this nest site revealed the remains of at least four springbok lambs. Ten of the farmers (27%) reported that eagles occasionally killed domestic lambs on their farms. The remaining nine farmers (24%) reported significant losses to eagles. Of these, three farmers described eight eye-witness accounts of eagles killing domestic lambs or kids. Most farmers considered that lambs were vulnerable to eagle attack up until 4 - 6 weeks old. One of the eye-witness accounts described a pair of black eagles and their fledgling killing a Merino lamb which was two and a half months old. However this incident and two others were recounted by a farmer who is renowned as something of a story-teller in Beaufort West. I have no grounds to refute the eye-witness accounts of the other two farmers, one of whom lost four Angora goat kids and one maltese poodle to a black eagle which he considered to be too old to catch hyrax. Surprisingly, this farmer refrained from killing the eagle and instead captured it in a padded gin trap for translocation. The other farmer saw a black eagle kill one of his 'stud' lambs close to a homestead. Most farmers considered both black and martial eagles to be responsible for stock losses, but some held martial eagles more responsible. Four farmers reported sudden incidences of lamb-killing by eagles which they attributed to drought and a decline in natural prey. Accounts of stock losses were varied by nature: 17 lambs recently; 9 lambs in one month; 14 carcasses under the eagles' nest; 14 goat kids etc.. Consequently it is not possible to accurately quantify the extent of stock predation by eagles in the Karoo from these reports.

Notions held by farmers in the present study were however very similar to those reported in other investigations. Farmers in Ladismith (Palmer unpubl.), Steytlerville (Anon 1992a unpubl.), Laingsburg and Philipstown (Siegfried 1963a), and in the Cape Province as a whole (Boshoff 1980) also maintained that eagle problems became manifest during drought due to low natural prey populations, and agreed that lambs were only really vulnerable to eagles during their first month. There are various indications that hyrax actually become more available to black eagles when conditions get more arid (pp. 274, 306-307), and I think that greater perception of predator problems by farmers during drought is probably prompted by high lamb mortality caused by drought. Questionnaire surveys have indicated that small-scale farmers tend to report higher losses to predators (Boshoff 1980; Nass et al. 1984). This might concur with observations in the present study that small-scale farmers are more sensitive and less tolerant to lamb-predation, and that areas of intense eagle persecution were low-income areas. Seventy one percent of Ladismith farmers claimed losses to eagles of up to 70 lambs per month, but no eagle-killed lambs were found on a follow-up investigation. Steytlerville farmers claimed that 5 - 100 goat kids were killed by eagles on their farms each season, and that losses in the district amounted to R140000 per annum. These claims have yet to be substantiated. Sixty four percent of Steytlerville farmers reported losses to eagles (75% in the mountainous areas)

University of Pretoria etd – Davies, R A G (1994)



and only 2% wished to conserve the birds. These reporting rates for stock losses to eagles are higher than those recorded during the present study (51% of farmers), and from the results of 13857 questionnaire returns, where 26% of Cape farmers claimed losses to eagles (Boshoff 1980). In the 1960's, a majority of Laingsburg farmers (71%) reported stock losses to eagles (mainly to black eagles), and a smaller portion of Philipstown farmers (37%) reported stock losses to eagles (mainly to martial eagles) in a questionnaire survey conducted by Siegfried (1963a). These questionnaire surveys have been used to glean information on the abundance of raptors (Boshoff & Vernon 1980), and on the persecution of raptors (Siegfried 1963a). They have also been used, especially in North American studies, to assess the proportion of lambs lost to predators and the relative contribution of mortality agents.

The portion of mortality that is attributed to predators is not a parameter that can be compared across studies because total mortality is so variable with environmental conditions. For instance, when conditions are excellent, predation may account for a large portion of mortality, but this might be misleading if overall losses are negligible. The indeterminable portion of lamb mortality is also highly variable in reports. For these reasons and for the purposes of this review I shall be expressing lamb losses to predators between birth and weaning as their proportion of the total born rather than of the total dying.

Summaries of such findings from questionnaire surveys are presented in Table 38. The percentage of lambs lost to predators is given for 11 surveys (in RSA and USA), and these yield an average figure of 6,65% lambs killed. This average is lowered to 5,22% if one 'problem flock' (see later) is omitted. The percentage of lambs lost to other causes is given for 7 surveys, and these yield an average figure of 8,91% lambs lost to other causes. The sum of these figures suggests that small stock farmers in South Africa and North America believe they lose 14-16% of their lambs between birth and weaning. Records at Grootfontein Agricultural College in the Karoo suggest a mortality rate of 10-12% for juvenile small stock in this region (Olivier *in litt.*). But farmers' estimates of total lamb mortality may be under-estimated due to the large number of newly-born lambs which disappear without a trace. Most studies indicate that 20%, or more, of lambs die between birth and weaning (Rowley 1970; Squires 1975; Houston 1977; Hewson 1984; Weir 1985).

Few stockmen carry out post-mortem examinations on lamb carcasses so losses to predators are usually based on signs of external feeding and tend to be exaggerated in these questionnaire surveys (Nesse, Longhurst & Howard 1976; Andrews & Boggess 1978; Sterner & Shumake 1978; Armentrout 1980; Boshoff 1980; Hewson 1981). Investigations which reveal that farmers' reports on stock losses to predators can be honest and accurate are in a minority (Balser 1974; Boggess *et al.* 1978; Schaefer *et al.* 1981; Robel *et al.* 1982). In the Swartberg mountains at the southern limit of the Karoo, sheep ranchers claimed they were losing up to 66 lambs each season to predators, and they estimated that the predators removed 11% of their lambs and that another 5% of the lambs died non-violently. A follow-up investigation by Bekker (*in litt.*), who carried out extensive post-mortem examinations, revealed that predation was the primary cause of death for less than one percent of lambs while other mortality factors were claiming as much as 15% of lambs born. Evidently the results of questionnaire surveys need to be interpreted with caution, but they do indicate that most ranchers see canids and possibly felids (in RSA) as the main threat to their livestock, rather than eagles (Table 38). This is exemplified by the numbers of livestock-loss claims that were allocated to respective predators by ranchers in Iowa (Table 39).

University of Pretoria etd – Davies, R A G (1994)

# TABLE 38
## FINDINGS ON THE PREDATION AND NEONATAL MORTALITY OF LAMBS FROM QUESTIONNAIRE SURVEYS OF RANCHERS

Losses refer to the percentage of total lambs born that die before weaning.
The relative importance of various predators in lamb-killing (as indicated by ranchers) is highlighted with asterixes.

| | | | | | | PREDATOR TYPE RESPONSIBLE FOR LOSSES | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SOURCE | REGION | BREED | SAMPLE SIZE | % LAMBS LOST TO PREDATORS | % LAMBS LOST TO OTHER CAUSES | EAGLES | UNSPEC. NON - EAGLE | CORVIDS | FOXES | JACKALS | COYOTES | DOGS | WOLVES | WILDCAT | CARACAL | PUMA | BEAR | BABOON | PIGS |
| Boshoff (1980) | Cape, RSA | various | 14761 farmers | | | ** | | *** | | **** | | | | *** | ***** | | | | |
| Lawson (1989) | Natal, RSA | various | 159 farmers | 3,4 | 6,4 | ? | | ? | | ***** | | **** | | | *** | | | * | |
| Bekker (in litt.) | Swartberg, RSA | various | 5 farmers | 11 | 5 | | | | | | | | | | | | | | |
| Reynolds & Gustad (1971) | four west states, USA | * whole flock | farmers | 5,3 | 16,1 | | | | | | | | | | | | | | |
| Dorrance & Roy (1976) | Alberta, USA | various | 75 farmers | 2,8 | 12,9 | | | | | | 95% | 3% | * | | | * | * | | |
| Early et al. (1974a & b) | Idaho, USA | * whole flock | farmers | 3,4 | 9,1 | | | | | | | | | | | | | | |
| Nielson & Curle (1970) | Utah, USA | * whole flock | farmers | 6,1 | | | | | | | | | | | | | | | |
| Gee et al. (1977) | 15 west states, USA | various | farmers | 8,1 | | | | | | | | | | | | | | | |
| U S Fish & Wildl. (1978): 1972-78 | Western states, USA | various | literature | 4 - 8 | | | | | | | ***** | | | | | | | | |
| Schrivner & Conner (1984) | Texas, USA | Angora kids | 101 farmers | 20,3 - 22,6 | | | | | | | ***** | | | | | | | | |
| Schaefer et al. (1981) | Iowa, USA | various | 1251 farmers | 5,2 | 5,9 | | | | | | ***** | *** | | | | | | | |
| Robel et al. (1981) | Kansas, USA | various | 109 farmers | 0,9 | 7,0 | | | | | | 224 | 54 | | | | | | | |



# TABLE 39
## FINDINGS ON THE PREDATION AND NEONATAL MORTALITY OF LAMBS FROM ANIMAL DAMAGE CLAIMS AND MISCELLANEOUS INCIDENTS

The relative importance of various predators in lamb-killing is shown by asterixes or by the number of claims/incidents.

| | | | | | | PREDATOR TYPE RESPONSIBLE FOR LOSSES | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SOURCE | REGION | BREED | SAMPLE SIZE | % LAMBS LOST TO PREDATORS | % LAMBS LOST TO OTHER CAUSES | EAGLES | UNSPEC. NON - EAGLE | CORVIDS | FOXES | JACKALS | COYOTES | DOGS | WILDCAT | CARACAL | BOBCAT | PUMA | BEAR | BABOON | PIGS |
| Lockie & Stephen (1959) | Scotland, UK | | incidents | | | 1 | | | | | | | | | | | | | |
| Lockie (1964) | Scotland, UK | | 21 prey | | | 3 | | | | | | | | | | | | | |
| Bergo (1987) | Norway | | 18 incidents | | | 1 | | | | | | | | | | | | | |
| Pearson & Caroline (1981) | Texas, USA | sheep & goats | claims | 0,27 flock | | | | | | | *** | | | | *** | | | | |
| Boggess Andrews & Bishop (1978) | Iowa, USA | various | 5800 claims | 1,5 | | | 2684 | | | | 6557 | 9068 | | | | | | | |

University of Pretoria etd – Davies, R A G (1994)



*Field necropsies*

Post-mortem examination of lamb carcasses in the field can yield more data on livestock predation than direct observations. Farmers' estimates of lamb losses to predators may be exaggerated when scavenging is mistaken for predation. The presence or absence of blood and bruising on a carcass is a sure sign of whether the lamb died violently or non-violently. Predation should not be considered the primary cause of death when the predation response is triggered by the weakened behaviour of a dying lamb. Thorough examinations of fresh carcasses will indicate whether a lamb was viable or not when killed (Rowley 1970).

An extensive carcass inspection survey still needs to be carried out in the Karoo. But in the course of fieldwork and visits to farms I had the opportunity of examining 23 lamb and kid carcasses where eagles were implicated as the main mortality agent. On 3 June 1987, I was called by a Karoo National Park ranger to investigate a lamb on the southern border of the park which had apparently been killed by an eagle. On arrival at the scene, an adult black eagle was flushed from the carcass of a Merino lamb which was thought to be approximately 15% of adult mass, i.e. about 8kg alive. A hindleg was missing and about three quarters of the carcass had been devoured. The carcass was very fresh and my first impression was that the eagle was indeed responsible for the death of the lamb. However, when we removed the carcass by vehicle, we flushed a Cape fox from nearby shrubs. On skinning the carcass we found matching bite wounds to the throat indicating that a small canid or felid had killed the lamb, and there was no massive haemorrhaging on the back or neck. This incident emphasized to me the ease with which scavenging by eagles can be mistaken for predation if a necropsy is not carried out.

Most of my visits to farms were prompted by landowners complaining of eagle problems. Despite this, only one visit in 29 yielded an opportunity to examine lamb carcasses for signs of eagle predation. Searches for lamb carcasses on other farms were unsuccessful, and it transpired that most of the farmers were referring to problems in the past when they called me out. In August 1988 however, Wynand Fourie of the farm Paardebond near Calitzdorp (in the Little Karoo) claimed that he was losing up to two goat kids per day to a black eagle (Allardice & Erasmus unpubl.). On this farm a Boer goat herd of 155 nannies was confined in a 130ha camp of degraded succulent karoo veld. Most nannies were giving birth in an area of 10ha. We advised Mr Fourie to place a shepherd with the kids. I joined Allardice and Erasmus in an investigation of Mr. Fourie's losses. These conservation officers had found no goat remains beneath the nearest black eagle eyrie. They had posted two observers in the kidding area for two days. A black eagle was roosting in the camp and fresh goat remains were found beneath the roost. No kills were observed, but on two occasions the eagle swooped low over a goat kid herd and was chased off by the shepherd.

During a search of the main kidding area, we found 22 goat kid carcasses which we examined in the field. Eighteen of these carcasses did not show any signs of damage by a predator or scavenger. Four carcasses had been fed on but cause of death was indeterminable for one. The absence of major subcutaneous haemorrhaging indicated that the three other carcasses were not killed by an eagle. There was evidence of carnivore predation on one of these. Droppings and triangular sections removed from the scapula indicated that the eagle had certainly fed from one carcass.

University of Pretoria etd – Davies, R A G (1994)



We ascribed the high kid mortality to the confinement of the nannies in an overgrazed environment. Many of the nannies that twinned were evidently abandoning one of their offspring. The habitat did not support many hyrax and did not afford nesting sites to eagles. In the absence of territorial birds it is not surprising that a non-breeding black eagle was attracted to the abundance of carrion. The eagle may have killed some unattended kids but we could find no direct evidence of this. Palmer (unpubl.) also found no evidence of lamb-killing by eagles when investigating an 'eagle problem' on farms in the Ladismith district. On one of these farms, high goat kid mortality to caracals attracted eagles and corvids in 1979-80, but post-mortem examinations of carcasses convinced the farmer that eagles were not responsible for the deaths in this case.

The findings of documented, field necropsy surveys in South Africa and other sheep-farming regions worldwide are summarised in Table 40. It is evident that of > 585 lamb carcasses examined in South Africa, none were considered to have been killed by eagles. This is despite the fact that these South African surveys were conducted in black eagle habitat. However, I have come across three undocumented reports of eagles killing lambs in South Africa which were confirmed by necropsies: black eagles may have been responsible for the death of one out of seven carcasses (including two ewes) examined by Brown (pers. comm.) in the early 1980's in the Underberg, Drakensberg; crowned eagles were certainly responsible for the death of two sickly five-week old lambs in April 1989 in the George District (S.J. Bekker pers. comm.); and black eagles killed one, possibly two lambs and seriously wounded another in September 1993 in the Kimberley District (Anderson & Esterhuizen pers. comm.). These reports were of isolated incidents where researchers were called out to investigate farmers' complaints. They did not comprise comprehensive surveys of lamb mortality. Although they indicate that eagles do kill lambs in South Africa, they do not afford quantitative data on the extent of this mortality factor for lambs in this part of the world.

The spread of estimates for lamb losses to predation are shown in Figure 103 for all questionnaire and necropsy surveys that I could access in the literature. As suspected, surveys by necropsy yielded generally lower estimates of predation. The average estimate of lamb predation in 32 surveys by necropsy was 4,91% of lambs born

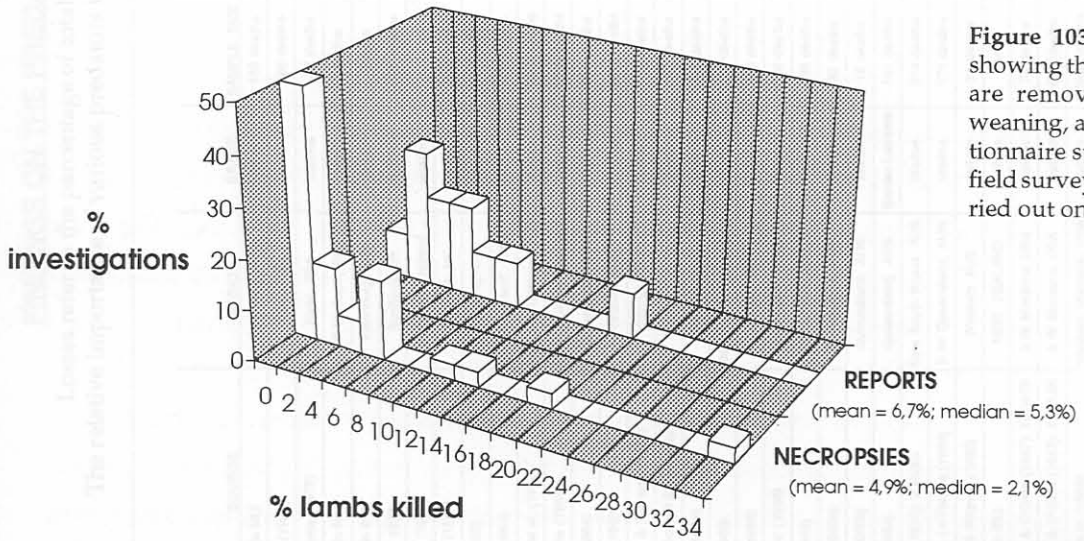



**Figure 103.** Frequency histograms showing the percentage of lambs that are removed by predators before weaning, as estimated from 11 questionnaire surveys (REPORTS) and 32 field surveys based on necropsies carried out on lamb carcasses.

University of Pretoria etd – Davies, R A G (1994)

# TABLE 40

## FINDINGS ON THE PREDATION AND NEONATAL MORTALITY OF LAMBS FROM FIELD NECROPSY SURVEYS

Losses refer to the percentage of total lambs born that die before weaning. Asterixes indicate where predation losses refer only to viable lambs.
The relative importance of various predators in lamb-killing is indicated by the number or percentage of lambs killed that could be attributed to those predators.

| | | | | | | PREDATOR TYPE RESPONSIBLE FOR LOSSES | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SOURCE | REGION | BREED | SAMPLE SIZE | % LAMBS LOST TO PREDATORS | % LAMBS LOST TO OTHER CAUSES | EAGLES | UNSPEC. NON - EAGLE | CORVIDS | FOXES | JACKALS | COYOTES | DOGS | WILDCAT | CARACAL | BOBCAT | PUMA | BEAR | BABOON | PIGS |
| Bekker (in litt.) | Swartberg, RSA | various | 133 deaths | 0,9* | 15 | | | | | 4 | | | | 54 | | | | | |
| Roberts (1986) | Natal, RSA | various | 395 deaths | | | | | | | 50 | | 330 | | 9 | | | | | |
| Rowe-Rowe (1975) | Natal, RSA | various | >57 deaths | <1,0 | | | | | | 57 | | | | | | | | | |
| Bekker (in litt.) | S W Cape, RSA | various | deaths | | 16,5 | | | | | | | | | | | | | | |
| Bekker (in litt.) | Elsenburg, RSA | various | deaths | | 16,0 | | | | | | | | | | | | | | |
| Houston 1977 | Scotland, UK | blackface | 297 deaths | 0,12* | | | | 24 | | | | | | | | | | | |
| Burgess (1963) | Northern England | unspec. | | 0,05%*? | | | | ** | | | | | | | | | | | |
| Hewson (1984) | Scotland, UK | blackface | 204 deaths | 0,7-2,8 | 25-46 | 11 | | | 26 | | | | | | | | | | |
| Weir (1985) | Scotland, UK | sheep | (800 deaths) | | | 2 - 9 (30) | | | unknown | | | 40 | | | | | | | |
| Moule (1954) | Queensland, AUS. | Merino | 453 deaths | 6,28 | 12,08 | | | >6 | | | | | | | | | | | >100 |
| Hughes et al. (1964) | New South Wales, AUS. | various | 3503 deaths | 0,64* | | | | | | | | | | | | | | | |
| McFarlane (1964) | New South Wales, AUS. | various | 3039 deaths | 1,96* | (18,04) | | | | | | | | | | | | | | |
| Smith (1964) | Queensland, AUS. | Merino | 981 deaths | 0,65* | | | | | | | | | | | | | | | |
| Dennis (1969) | Western AUS. | various | 4417 deaths | 0,54* | | | | | | | | | | | | | | | |
| McHugh & Edwards (1958) | Victoria, AUS. | various | 512 deaths | 0,95* | 6,05 | | | | | | | | | | | | | | |
| Moore, Donald & Messenger (1966) | Southern AUS. | Merino | 157 deaths | 3,0* | 21,80 | | | | | | | | | | | | | | |
| Davies (1964) | Western AUS. | Merino | 308 deaths | 7,0* | 20,18 | | | | | | | | | | | | | | |
| Anon (1965) | New South Wales, AUS. | Merino | 323 deaths | 1,2* | 12,38 | | | | | | | | | | | | | | |
| Turner (1965) | Victoria, AUS. | Polwarth | 260 deaths | 2,15* | 15,89 | | | | 31 | | | | | | | | | | |
| McDonald (1966) | Melbourne, AUS. | Polwarth | 390 deaths | 12,2* | 24,45 | | | | @129 | | | | | | | | | | |
| Anon (1968) | Southern AUS. | various | 695 deaths | 0,13* | 9,26 | | | | | | | | | | | | | | |
| Smith (1965b) | Queensland, AUS. | Merino | 32 deaths | 6,4* | 2,54 | | | | | | | | | | | | | | |
| Smith (1965b) | Queensland, AUS. | Merino | 18 deaths | 2,2* | 4,27 | | | | | | | | | | | | | | |
| Smith (1964) | Queensland, AUS. | Border-Leiceste | 131 deaths | 15,3* | 27,23 | | | 30 | | | | | | | | | | | |
| Rowley (1970): 2 flocks | New South Wales, AUS. | Merino | 314 deaths | (1,96*) | (34,22) | 5 | | 73 | 44 | | | | | | | | | | |
| Jordan & Le Feuvre (1989) | S W Queensland, AUS. | Merino | 171 deaths | 1,2 - 2,0* | >15,0 | 1 | | | 8 | | | | | | | | | | 11 |
| Brooker & Ridpath (1980) | Western AUS. | various | 53 deaths | | | 5 | 1 | | 5 | | | | | | | | | | |
| Bekker (in litt.) | NEW ZEALAND | various | deaths | | 16,0 | | | | | | | | | | | | | | |
| Matchett & O'Gara (1987): 1974-75 | S W Montana, USA | various | 73 deaths | (38) | (6) | 59 | 3 | | | | | | | | | | | | |
| Matchett & O'Gara (1987): 1976-85 | S W Montana, USA | various | 865 deaths | (3) | (16) | 59 | 74 | | | | | | | | | | | | |
| O'Gara et al. (1983) | Western Montana, USA | various | 1944 deaths | 20,8 | 11,5 | 2 | | 6 | 7 | | 854 | 6 | | | | | | | |
| Wiley & Bolen (1971) | Southwestern USA | * whole flock | 23 deaths | | | 3 | >1 | | | | | | | | | | | | |
| Bowns et al. (1973) | Utah, USA | spring lambs | 236 deaths | 0,8 | 1,6 | | | | | | 71 | | | | | | | | |
| Bowns et al. (1973) | Utah, USA | summer lambs | 371 deaths | 6,6 | 1,2 | | | | | | 238 | | | | | | | | |
| Taylor et al. (1979) | Utah, USA | lambs | 3345 deaths | 5,8 | 3,6 | | | | | | 3144 | (50) | | | | (50) | (50) | | (50) |
| Klebenow & McAdoo (1976) | Nevada, USA | * whole flock | 351 deaths | (4%) | (5%) | 1 | | | | | 110 | 2 | | | 3 | | | | |
| Tigner & Larson (1977) | Wyoming, USA | lambs | 3600 deaths | 2,3 | 5,0 | * | | | | | 77% | * | | | * | | * | | |
| Schrivner et al. (1985) | California, USA | unspecified | 953 deaths | 2,7 - 10,4 | | 5 | | | | | 665 | 63 | | | | 5 | 6 | | |
| Schaefer et al. (1981) | Iowa, USA | various | 227 deaths | | | | | | | | 129 | 95 | | | | | | | |
| Glover & Heugly (1970) | Texas, USA | lambs | | 1 - 2 | | | | | | | | | | | | | | | |
| Glover & Heugly (1970) | Texas, USA | kids | | <25% | | | | | | | | | | | | | | | |
| Littauer & White (1981) | New Mexico, USA | various | | | | | | | | | | | | | | | | | |

University of Pretoria etd – Davies, R A G (1994)



(median=2,06). This average is influenced equally by extensive surveys and by surveys of small problem flocks. When each survey is weighted in accordance with the number of carcasses examined (nearly 30000), the average estimated loss to predation is 3,91% of lambs born. The average estimate of lambs lost to other causes among the same surveys is 13,7% of lambs born (or 11,2% when weighted in accordance with sample size). These figures suggest that farmers do tend to over-estimate predation and under-estimate other losses.

The surveys indicate some variation in lamb predation between the major sheep-farming regions. The results of all documented field studies of lamb mortality by necropsy are summarised by geographical region in Figure 104. Evidently ranching operations in Australia and especially South Africa and Scotland experience relatively low losses of lambs to predators, whereas North American operations experience relatively high losses. This can be attributed partly to severe problems with coyotes in some of the United States.

The most detailed and extensive investigations of lamb mortality have been carried out in Australia (nearly 16000 necropsies). Many of these studies were routine investigations of flocks rather than problem situations. Under the influence of pioneering methods (Alexander 1964; McFarlane 1965), nearly all of the Australian studies have distinguished true predation of viable lambs from the removal of dying animals by predators. As Rowley (1970) points out, "Since lamb starvation is usually irreversible, for economic reasons, in Australia, it is financially insignificant whether or not a predator hastens the inevitable end; this situation could have been avoided if the onset of starvation had been prevented". Most American studies did not distinguish between the killing of lambs that were dying already and the killing of healthy lambs, and this is probably mostly responsible for the high rate of loss of lambs to predators reported in this region. The average loss of lambs to predators, taken from 17 Australian surveys involving necropsies, was 3,77% of lambs born (s.d.=4,35; median=1,96%). The most extensive carcass surveys indicated lower levels of predation. So a weighted average of 1,66% of lambs lost to predators (in accordance with the number of carcasses examined) includes problem situations but is not unduly influenced by them. The average loss of lambs to other causes, taken from 14 Australian surveys involving necropsies, was 16,0% of lambs born (s.d.=9,1; median=15,7). This estimate was not much changed when sample size was taken into account (16,8%).

These discussions pertain to lamb predation by all types of predators. Where accessible, I noted the amount of lambs lost to different types of predators in these surveys by necropsy (Table 40). In Figure 104 the number of lambs lost to various predator types are shown for the different major sheep-farming regions. It is clear that wild and domestic canids cause the most damage to ranching operations. In South Africa caracals *Felis caracal* cause significant losses, and in Australia feral pigs *Sus scrofa* are significantly involved. Avian predation was less frequent than mammalian predation in all regions and losses to corvids exceeded those to eagles. Only in Scotland were eagles significantly involved in livestock predation, but this is based on only three studies and overall losses to predators were exceptionally low. Eagles were least involved in livestock predation in South Africa.

Black, martial and crowned eagles are all highly territorial, and are not inclined to scavenge. There are no records of these eagles being attracted in large numbers to an abundance of dead or dying lambs, unlike golden eagles and wedge-tailed eagles. It is important to bear in mind that these estimates of the relative responsibility of eagles in lamb-killing are based on all records of lambs killed (healthy or sick). It may be that eagles are more likely to attack

University of Pretoria etd – Davies, R A G (1994)



weak and sickly lambs than the larger and possibly more powerful carnivores, in which case eagles would be responsible for a smaller proportion of the viable lambs killed by predators than indicated.

| Region | Number of carcasses examined | % lambs lost to predators | % lambs lost to other causes | total lambs lost | % kills made by eagles |
|---|---|---|---|---|---|
| RSA | 191 | 0.9 *(healthy)* | 16.15 | 17.05 | 0 |
| UK | 1423 | 0.32 *(healthy)* | 35.5 | 35.82 | 15.9 |
| AUS | 15704 | 1.66 *(healthy)* | 16.81 | 18.47 | 2.46 |
| NZ | ? | ? | 16 | ? | 0 |
| USA | 12660 | 6.42 *(all)* | 6.42 | 12.92 | 2.25 |
| WORLD | 29978 | 3.91 *(mixed)* | 11.23 | 15.14 | 2.38 |

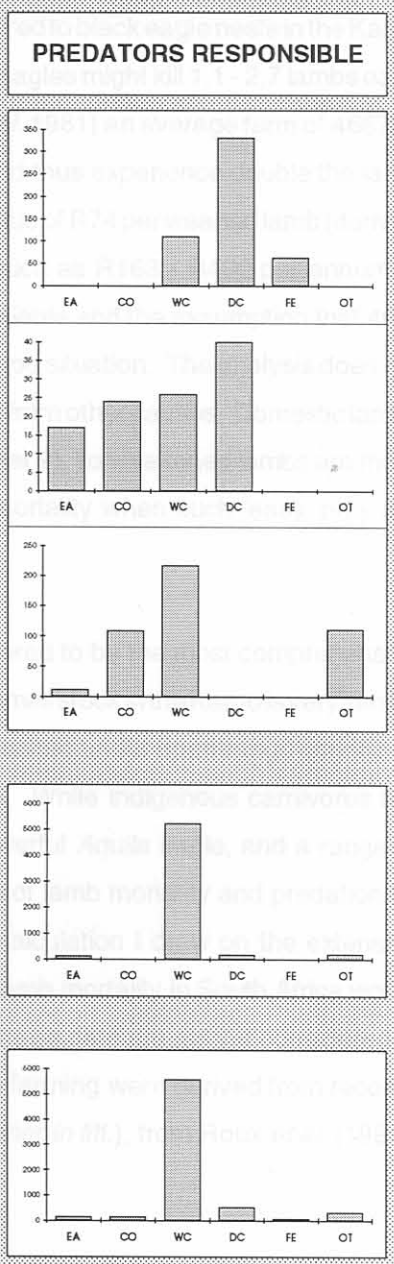



**Figure 104.** The findings of worldwide field necropsy surveys on lamb mortality summarised by geographical region (LEGEND: RSA - South Africa; UK - Scotland; AUS - Australia; NZ - New Zealand; USA - United States of America; WORLD - all surveys combined). Column 2 gives an indication of the extent of these surveys but it refers only to lambs dying and not to the total number of live lambs monitored. The percentage lambs lost to predators (Column 3) refers to the period between birth and weaning - I have indicated whether these estimates include all lambs killed by predators, or only viable (healthy) lambs. These estimates can be added to lambs dying non-violently (Col. 4) to give the percentage of total lambs lost (Col. 5). The histograms to the far right indicate the relative involvement of the different types of predators in lamb-killing (healthy or sick) for all surveys which provided such information (KEY: EA - eagles; CO - corvids; WC - wild canids; DC - domestic canids; FE - felids; OT - other e.g. pigs in AUS, bears in USA). The percentage involvement of eagles is listed in column 6.

University of Pretoria etd – Davies, R A G (1994)



*Economics of livestock predation by black eagles in the Karoo*

As mentioned earlier, the collections of prey remains suggested that breeding pairs of black eagles on karoo farmland may be delivering 2,8 - 6,7 lambs to their nests each year. This estimate is prone to much bias discussed earlier and in Chapter 9. If we assume that the feeding habits of black eagles on karoo farmland are similar to those of golden eagles on scottish farmland (see earlier), and that 40% of lambs delivered to black eagle nests in the Karoo were killed rather than scavenged, this would imply that a resident pair of black eagles might kill 1,1 - 2,7 lambs each year. In strictly mountainous terrain (which spans 15% of the Karoo: Roux *et al.* 1981) an average farm of 4687ha could accommodate two black eagle territories (2300ha each - Chapter 6), and thus experience double the lamb killings estimated for a single pair. With this reasoning and at a current market value of R74 per weaned lamb (derived from Table 41, overleaf), black eagles might be costing karoo farmers as much as R163 - R400 per annum in mountainous districts. However, this estimate of lamb predation is not very reliable and the assumption that 40% lambs are killed rather than scavenged is very arbitrary for the black eagle - Karoo situation. The analysis does not take into account the possibility that some of the lambs killed were already dying from other causes. Domestic lambs are close to the upper limit of prey size that black eagles prefer to attack (Chapter 9), so weakened lambs are more likely to elicit predation especially during the period of high neonatal lamb mortality when such 'easy' prey are abundant.

For reasons given above, the Australian surveys of lamb mortality are considered to be the most comprehensive and detailed, and the least biased (towards problem situations). The farming of small stock in the Karoo is very similar to that in Australia. Merino sheep are the preferred breed, and these are maintained under open-range conditions and low stocking rates in drought-prone southern hemisphere environments. While indigenous carnivores are scarce in Australia, lambs are still exposed to corvids, an abundant and powerful *Aquila* eagle, and a range of introduced meat-eaters including foxes and feral pigs. No extensive surveys of lamb mortality and predation by necropsy are available for the Great Karoo. So in the following economic calculation I draw on the extensive Australian research on the grounds of the given similarities. Current data on lamb mortality in South Africa would indicate lower rates of loss to predators, and less involvement of eagles. But these data are not yet considered to be sufficiently complete for the following calculations. The statistics on karoo farming were derived from records held by the Department of Agriculture at Grootfontein, Middelberg, Karoo (Olivier *in litt.*), from Roux *et al.* (1981), and Anon (1992b).

Total extent of the karoo agricultural region (in South Africa) is 29 062 000ha. Within this area there are 8972 farms owned by 6200 farmers. On average, individual karoo farmers manage about 4687ha. Population parameters for the major classes of small stock in the Karoo and on the average karoo farm are given in Table 41 (overleaf). About 819 new lambs or kids are born from these small stock on the average farm each year. At predation and non-violent mortality rates of 1,66% and 16% respectively, one would expect that 13,6 of these lambs would be killed by predators before weaning, and that 131 would die from other causes over the same period. Most of this mortality would occur within two weeks of birth. In mountainous regions this means that about 70 dead lambs would be available to each resident pair of black eagles as carrion in one or two major pulses each year.

University of Pretoria etd – Davies, R A G (1994)



TABLE 41

A SUMMARY OF THE NUMBERS AND ANNUAL MORTALITY OF SMALL LIVESTOCK IN THE KAROO AND ON THE AVERAGE FARM FOR CALCULATING THE ECONOMIC SIGNIFICANCE OF PREDATION

Information sources for livestock numbers and population composition are given in the text. The last four columns refer to an analysis representing the average karoo farm. The number of lambs dying non-violently (column 10 - 16% of total) and to predation (column 11 - 1,66% of total) between birth and weaning were based on the results of extensive, detailed Australian research on the open-range farming of Merino sheep, which was considered to be most appropriate for the karoo situation (in the absence of sufficient local information).

| LIVESTOCK CLASS | Rand value per weaned lamb | Karoo nos. | Average farm nos. | Ppn. adult female | Lambs produced per adult female/yr | Karoo lamb nos. | Farm lamb nos. | Total no. dying per year | No. dying from other causes/yr | No. killed by predators per year | estimated annual value (Rands) of predation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Woolled sheep | 60 | 4745363 | 765.38113 | 0.6 | 0.7 | 1993052 | 321.460 | 56.7698 | 51.4336 | 5.33624 | 320.174 |
| Mutton sheep | 90 | 3449110 | 556.30806 | 0.7 | 1 | 2414377 | 389.416 | 68.7708 | 62.3065 | 6.46430 | 581.787 |
| Angora goats | 35 | 959803 | 154.80694 | 0.6 | 0.6 | 345529 | 55.7305 | 9.84201 | 8.91688 | 0.92513 | 32.3794 |
| Boer goats | 75 | 354996 | 57.257419 | 0.7 | 1.3 | 323046 | 52.1043 | 9.20161 | 8.33668 | 0.86493 | 64.8698 |
| TOTAL | | 9509272 | 1533.7535 | | | 5076005 | 818.710 | 144.584 | 130.994 | 13.5906 | 999.210 |

The overall cost of predation on viable lambs, to the average karoo farmer, is estimated to be 13,6 lambs at a current market value of R999 (U.S.$ 289). Only a fraction of this cost can be attributed to eagles. If we assume that lamb predation by black or martial eagles in the Karoo occurs in similar proportion to lamb predation by eagles worldwide (American and Australian studies were very similar in this regard - see Fig. 104), then the overall cost of eagles to the average karoo farmer is estimated to be 0,32 lambs with a current market value of R 23,78 (U.S.$ 6,88). This figure is more likely to be over-estimated than under-estimated because current limited data indicate lower rates of lamb losses to predators in South Africa (Fig. 104), and because black and martial eagles are not known to converge (in numbers) on lambing paddocks, as has been observed for golden eagles in America and wedge-tailed eagles in Australia. This estimate of the cost of eagles to karoo farmers is free from the bias and arbitrary assumptions of the earlier estimate, and is the most considered (upper) indication for the overall cost of true predation (of viable lambs) by eagles in the Karoo, be they martial eagles on the plains or black eagles in the mountains.

*Managing problem situations*

The previous calculations can give an indication of the scale of the problem, but most studies indicate that it is not appropriate to consider lamb predation in overall or average terms. The variation in lamb predation rates from Australian field necropsy surveys, as represented by their standard deviation, was roughly equivalent to their mean. This indicates that lamb predation was not evenly dispersed from flock to flock. The high incidence of low predation rates and low incidence of high predation rates as revealed among the necropsy surveys in Figure 103, is typical of a poisson distribution. The same phenomenon has been noticed by Wagner (1972), Wagner & Pattison (1973), Balser (1974), Dorrance & Roy (1976) and Gee *et al.* (1977). Over 80% of all predator losses in Kansas were reported by only 22% of questionnaire respondents (Robel *et al.* 1981).

University of Pretoria etd – Davies, R A G (1994)


These observations confirm the sporadic occurrence of problem flocks or situations. A number of the example studies given in Tables 38 - 40 which yield high estimates of predation can be described as such. For instance the ranches in southwestern Montana where coyotes were killing up to 12 lambs per night (O'Gara *et al.* 1983), and where golden eagles caused such extensive damage (Matchett & O'Gara 1987). Usually, extenuating circumstances can be found which explain these high predation rates: aggregations of young eagles after a crash in natural prey in the latter instance; high losses to foxes in Australia were associated with a toxic element and overgrazing in one case (McDonald 1966), and a 'killer' or rogue fox in another (Turner 1965); conspicuous lambs of Border Leicester sheep were found to be highly susceptible to disease after attack by ravens (Smith 1964), etc..

The golden eagle predation described by Matchett & O'Gara (1987) is the only serious problem situation that I found in the literature where eagles were held responsible. Aside from a few isolated lamb kills, there have been no confirmed 'problem situations' to date where African eagles were involved. In two cases, claims of severe lamb predation by black eagles proved unfounded (Palmer unpubl.; Allardice & Erasmus unpubl. / the present study). A similar claim has been lodged in the Steytlerville district but this has yet to be investigated. Farmers from this district do claim to have seen aggregations of up to 30 black eagles at a time. There are no such records in the abundant ornithological literature on this highly territorial species, so this claim is likely to be the result of exaggeration or confusion (possibly with white-necked raven). Despite this, two post-mortem examinations of lamb carcasses and a couple of credible eye-witness accounts of kills indicate that black eagles have killed lambs in the past and will do so again. One cannot expect a few unlucky farmers to tolerate unusually high levels of livestock predation on the basis that predators do little damage overall. Management techniques which can be expected to help minimise any lamb losses to eagles are now considered.

Much effort at reducing the threat of eagle depredation in the past has been geared towards managing eagles rather than managing lambs. The shooting incidents described earlier represent this in the extreme, and current, localised 'blanket control' of eagles is ineffective at diminishing numbers. Furthermore, removal of resident territorial eagles might allow an influx of immatures and non-breeding adults which may be more prone to kill lambs. Other indiscriminate methods of predator control such as poison and gin traps are ineffective and inhumane methods for controlling problem animals, but they may be highly damaging to vulnerable non-target wildlife species. Their use on South African rangelands should be discontinued and they should be replaced by more selective methods such as toxic collars, cage traps, and padded gin traps. Problem animal control should move from the concept of problem species to that of problem individuals (Stuart 1987b).

Four karoo farmers reported to me that they used padded gin traps, and any eagles they caught were sent to nature conservation officers for translocation. Conservationists with the responsibility for solving conflicts between wildlife and domestic stock, have favoured this less drastic course of action whereby 'problem' eagles are captured unharmed and transported for release in other areas, preferably devoid of livestock. A growing body of evidence however, indicates that this is not a satisfactory option. Of eight eagles which were moved up to 290km in the Cape and then seen or recaptured once again, five (63%) had returned to their original site of capture (Boshoff & Vernon 1988). Of 14 golden eagles which were moved 416 - 470km in and around Wyoming and then seen or recaptured again, twelve (86%) had returned to their original site of capture, and most of these were able to regain their territories

University of Pretoria etd – Davies, R A G (1994)



and mates despite rapid replacement from the non-breeding population (Phillips, Cummings & Berry 1991). Neimeyer (1977 unpubl.) also noted the return of translocated golden eagles. Areas devoid of livestock are usually conservation areas which already have resident eagle populations, so 'problem' eagles released into these situations will often be displaced into neighbouring farmland where they may continue a lamb-killing habit and antagonise farmers who were previously well-disposed towards eagles. An eight-year programme involving the translocation of 432 golden eagles from a problem area failed to reduce eagle depredations on livestock and cost an estimated U.S.$ 112 771 - "Eagle translocation is a reactionary measure, does not prevent depredation, could be expensive if large numbers of eagles were involved and may only transplant the problem, not solve it" (Matchett & O'Gara 1987).

In a comprehensive assessment of methods to control eagle depredations on livestock, Matchett & O'Gara (1987) found that neither taped eagle alarm calls nor sporadic harassment of eagles in lambing areas by aircraft and by using explosive charges were practical or effective at reducing depredations. Human activity has however sometimes proved a deterrent to eagles (McAdoo & Klebenow 1978; O'Gara & Matchett 1985 unpubl.). A karoo farmer reported to me that shooting just behind black eagles was usually sufficient to scare them away from lambing camps (Morgan *in litt.*).

Taste aversion is a possible option for reducing livestock predation by eagles. Birds especially can show extremely rapid aversion to a particular prey type after only one unpleasant experience, and the effectiveness of such anti-predator strategy is evident in the extent of mimicry of distasteful aposematic species among insects (Brower *et al.* 1968; Brower 1969, 1984). Juvenile sheep and goats are very distinct from natural eagle prey in looks, so it is conceivable that eagles might learn to avoid these prey types if they experience illness after eating them. Lithium chloride has been used as a taste-aversion agent to reduce stock losses by coyotes with mixed results (Griffiths, Connolly, Burns & Sterner 1978; Burns & Connolly 1980; Burns 1983a, 1983b), but it has successfully caused taste-aversion for particular prey types in red-tailed hawks *Buteo jamaicensis* and great horned owls *Bubo virginianus* (Brett, Hankins & Garcia 1976; Cheney, Vander Wall & Poehlmann 1987).

In response to farmers' requests for assistance in dealing with eagle problems, I drew up recommendations for the use of lithium chloride based on these studies whereby lamb carcasses should be treated with two injections of lithium chloride solution, one into the shoulder and one into the rump, which would amount to a total dose of 250mg lithium chloride. If a black eagle was to consume the entire carcass it would receive a maximum oral administration equivalent to 63mg lithium chloride per kg body weight. The dosages used by Cheney *et al.* (1987) which led to taste-aversion were approximately 40mg lithium chloride per kg body weight. These recommendations were distributed to eleven farmers in the Cape and Orange Free State by myself and by Nature Conservation Officers, but no rigorous examination of the trials were carried out. Brand (1992) assessed the results of these trials as largely inconclusive, but taste-aversion may have occurred in one instance.

Three dead jackal buzzards were picked up around two of the treated carcasses which Brand (1992) attributed to lithium chloride poisoning, on the basis that certain small birds have been known to voluntarily consume lethal amounts of the substance in captivity (Rogers 1974). Raptors however, regularly regurgitate pellets and the

University of Pretoria etd – Davies, R A G (1994)



regurgitation process should be stimulated by the strongly emetic nature of lithium chloride (Burns & Connolly 1980). Black eagles feeding on the treated lamb carcasses were observed to vomit (Brand 1992). If the recommended dosages were adhered to, the jackal buzzards in question could not have received more than 290 mg lithium chloride per kg body weight, even if one bird consumed the entire lamb carcass which is very unlikely. Red-tailed hawks survived intramuscular injections of lithium chloride at dosages of up to 320mg per kg body weight without any serious negative consequences (Brett *et al.* 1976) - these birds could not get rid of the lithium chloride by vomiting. It therefore seems highly improbable that lithium chloride caused the death of the jackal buzzards unless the recommended dosages were greatly exceeded and the birds, for some reason, were unable to regurgitate. Unfortunately, no necropsies were carried out on the dead jackal buzzards. I would have to agree with Brand (1992) though, that at this stage field trials of taste-aversion in eagles using lithium chloride are inconclusive, and they should be postponed until captive trials have demonstrated whether this method is practical for use on wild raptors. Captive trials are currently being planned by Dr. E. Verreyne (P.O. Box 1667, Kuruman 8460, Cape Province).

More recent studies suggest that the emphasis of management to reduce lamb predation should shift from attempts at managing predators to improved management of the flock (Hewson 1984; C.J. Brown pers. comm.). An obvious and immediate advantage in management to reduce losses to eagles, is that eagles only pose a serious threat to very young lambs (Arnold 1954; Wiley & Bolen 1971; Tjernberg 1981; Hewson 1984), and these are normally only available for 6 - 8 weeks each season. Intensive management over this short period may well prove worthwhile. Penning sheep in corrals reduced losses to predators in North America (Robel *et al.* 1981) and Namibia (C.J. Brown pers. comm.), and would undoubtedly reduce the threat of eagle predation in the Karoo but is not practised in this region any more. By far the simplest and most effective management technique to prevent eagle depredations in the Karoo is to place a shepherd with the flock during the crucial lambing period. All the farmers around Beaufort West who used this management practice did not experience problems with eagles. To be effective, shepherding must be carried out in a lambing camp which is not too large to patrol.

Unfortunately, many open-range sheep flocks in the Karoo are not very habituated to humans. Failure of the ewe-lamb bond is the biggest killer of young lambs (Rowley 1970), so any human disturbance which may lead to desertion of lambs is highly undesirable. For unhabituated flocks, scarecrows may prove to be a good option (O'Gara & Matchett 1985 unpubl.). Matchett & O'Gara (1987) showed experimentally that the use of scarecrows could alter the dispersion patterns of aggregating golden eagles and reduce lamb predation rates tenfold. This was despite a greater availability of young lambs in the areas where scarecrows were used. The authors emphasised that scarecrows should only be erected for the crucial lambing period, close to the bedding grounds. Moving the scarecrows and attaching shiny objects to them may help prevent eagles from becoming habituated to them.

It has also been suggested that lambing should take place outside of the eagle breeding season and away from areas of eagle activity (Anon 1987; Anon 1992a unpubl.). However, farmers complain that lambing seasons are geared to the maximum reproductive output of the flock and should not be changed. Indeed, autumn matings (late winter lambings) can double the reproductive output of ewes in some regions if supplements are provided (Roux *et al.* 1981), but for various reasons spring matings and autumn lambings (March - April) are preferred in the Beaufort West district. Although this lambing schedule may bring resident eagles into breeding condition early (Chapter 6), it means

University of Pretoria etd – Davies, R A G (1994)



that lambs are past their vulnerable first month by the time breeding eagles have nestlings to feed. Careful attention needs to be given to spring lambings to avoid the crucial imprinting phase of eagle nestlings (July - August), and lambing flocks should be moved away from eagle nesting areas and shepherded. Two farmers adjoining the KRNP said they reduced losses to eagles by simply moving their flocks away from the hills during lambing (Mocke & Nel, pers. comm.). This appears to be a common, effective and practical management option.

In at least two cases black eagles have been attracted to a lambing area by high mortality of the lambs to other causes (Palmer unpubl.; Allardice & Erasmus unpubl. / present study). In similar circumstances, golden eagles turned to lamb predation when lamb carrion was temporarily unavailable (O'Gara *et al.* 1983). Basic veld and flock management which ensures enough food and shelter for lambing flocks will impede the major mortality factors and ensure a healthy lamb crop. In consequence there will be less carrion to attract eagles and more natural prey to hold their attention. It is important to realise that eagle chicks may be likely to wed or imprint to a lamb diet whether lambs are scavenged or killed by the eagles. So the removal of any lamb carcasses from the lambing camps is an excellent and very feasible management practice (Robel *et al.* 1981; O'Gara et al. 1983), especially when high mortality is unavoidable due to disease or climate. Natural removers of carcasses such as Cape vultures which have been eradicated from the Karoo by the indiscriminate use of poison (Allan 1989) should be restored to their former haunts.

University of Pretoria etd – Davies, R A G (1994)



# CONCLUSION

It is a common notion held by karoo farmers that eagles are responsible for sometimes extensive depredation of their lambs. The present study indicates that scavenging on livestock carcasses is prevalent among karoo black eagles but two investigations of 'problem situations' involving black eagles (Palmer unpubl. and the present study) using limited necropsy surveys demonstrated no direct evidence of lamb-killing by the eagles. Larger scale necropsy surveys in South Africa provided no evidence of lamb-killing by eagles, but such surveys still need to be done in the Great Karoo, in the Steytlerville district and in the northern Cape. Using best estimates of lamb predation rates and the relative involvement of eagles, it is calculated that the removal of viable lambs by eagles costs the average karoo farmer less than R24 per annum (0,32 lambs).

As a possible explanation for this extremely low incidence of lamb-killing by eagles, it is suggested that unlike other predators, the majority of eagle chicks are fed on natural prey items during sensitive developmental phases and so become imprinted or wedded to natural prey. Sheep-farming in the mountainous regions of the Karoo might be expected to experience greater losses to avian predators if these regions were not patrolled by the highly prey-specific black eagle which excludes conspecifics and other large eagles from breeding territories. Karoo plains are patrolled by a more generalist avian predator, the martial eagle, which may be more inclined to take domestic stock but which occurs at extremely low density (Van Zyl 1992). Neither species is known to converge on lambing paddocks.

Although lamb killing by eagles in the Karoo is very rare, some evidence confirms that it does occur and it is probable that such losses would be concentrated on a minority of farms. Large-scale efforts involving indiscriminate persecution of predators to reduce such losses appear futile, and are highly damaging to vulnerable non-target species. It is suggested that efforts to manage predators (including translocation of eagles) be replaced by more intensive management of flocks, especially during the short, vulnerable lambing season. Shepherding or the use of scarecrows, and moving lambing flocks away from areas of eagle activity are probably the most effective and practical options. But taste-aversion may prove useful in the future. In the prevention of a lamb-killing trait amongst eagles, it is important that vulnerable young lambs be unavailable to breeding eagles when they are feeding young nestlings going through sensitive developmental phases. For black eagles in the Karoo this critical period would be July and August, so special attention needs to be given to spring lambings. The removal of carcasses from lambing camps will remove an incentive for predation and will help prevent eagle chicks from becoming wedded to lambs as prey. If lamb losses to eagles persist despite intensive flock management, the culprits should be removed from the population to prevent the inheritance and spread of a lamb-killing trait. Zoological gardens, captive breeding institutions and falconers should be considered as destinations for these eagles.

On the grounds that lamb-killing by eagles in the Karoo is very rare and of negligible financial importance overall, and on the basis that any localised eagle problems can be dealt with, I would argue that black eagles are certainly compatible with the open-range farming of small stock in the Karoo, especially if one considers the beneficial effects of black eagles to sheep grazing (Chapter 12).

University of Pretoria etd – Davies, R A G (1994)



*CHAPTER 12*

# *BLACK EAGLE PREDATION AS A FACTOR INFLUENCING ROCK HYRAX POPULATIONS*

## INTRODUCTION

To test the claim by naturalists that eradication of predators such as eagles led to irruptions of hyrax in the past (e.g. Thomas 1946; Kolbe 1967; Rubidge in Kolbe 1983), and to establish the ecological role of black eagles on karoo farmland, requires a comprehensive examination of the impact of eagle-predation on rock hyrax in relation to other factors that lead to loss or addition of individuals to the prey population. The influence of predators on their prey (and *vice versa*) has been a dominant theme in empirical and theoretical ecology (Berryman 1992), perhaps giving rise to more literature than any other ecological topic (Matson & Berryman 1992). The ability of predators to 'control' their prey has been especially questioned for vertebrate communities, with early researchers complaining that the debate was 'generating more heat than light' (Gabrielson in Craighead & Craighead 1956). Numerous field studies, experimentation, and recent modification of general predator-prey theory are now presenting a clearer picture for the role of predation, but disagreements still persist (for example compare Erlinge *et al.* 1984 with Kidd & Lewis 1987, or Ballard, Whitman & Reed 1990 with Boutin 1992).

Much empirical and theoretical research on predation and other factors affecting vertebrate prey populations has been directed at trying to understand cyclicity among certain far northern hemisphere prey populations. Best known are the 10y cycle for snowshoe hares and associated species in North America (Elton & Nicholson 1942; Keith, Todd, Brand, Adamick & Rusch 1977; Keith, Cary, Rongstad & Brittingham 1984), and the 4y cycle for microtines and associated species in northern Europe (Erlinge *et al.* 1983; Liberg 1984; Henttonen, Oksanen, Jortikka & Haukisalmi 1987; Hansson & Henttonen 1988; Korpimäki 1993). These cycles have provided a focal point for study of the factors that affect prey population dynamics and a brief account of this research will provide a useful framework for the discussions in this chapter. A multitude of explanations have been offered for the phenomenon of cycles (for reviews see: Bulmer 1974; Lidicker 1988; Akçakaya 1992). In the 1950's and 1960's abiotic and then intrinsic mechanisms of population regulation were the most popular explanations (e.g. Christian 1950; Chitty 1960), but intrinsic mechanisms could not explain cyclicity in non-microtines (Hansson 1984; Henttonen 1985; Korpimäki 1986; Korpimäki & Norrdahl 1989a), nor the synchrony and the regional variation in the amplitude of cycles (Hansson 1988b). Much information gathered from field studies has been published in the 1980's and it is now becoming accepted that predation and refuge play key roles in the pattern of cycles, while depletion of food supplies and possibly disease may be involved in initiating the decline from peak prey densities.

Early predator-prey theory evolved prior to this knowledge but also found focus on population cycles at times. Oscillations of predator and prey populations were a feature of the earliest predator-prey model derived by Lotka (1925) and then Volterra (1928, translated in Chapman 1931) from Verhulst's (1838) 'logistic' equation. But the

University of Pretoria etd – Davies, R A G (1994)


Lotka-Volterra equations worked on the chemical principle of mass action whereby the population responses were proportional to the product of their biomass densities. Consequently, the oscillations in this early model were neutrally stable and were highly dependent on initial conditions. This problem was passed on to subsequent predator-prey models, and a series of theoretical propositions (functions of predator interference, prey refuge etc.) were incorporated to confer stability (equilibria or stable limit cycles) on the basic model (e.g. Nicholson & Bailey 1935). Most of the early predator-prey models were based on laboratory studies and simulations of insect parasitoid interactions, so they were far removed from the biological data that were accumulating from a progression of field studies on vertebrate predator-prey interactions (Hansson 1988a; Akçakaya 1992).

While the theoretical study of predation was evolving, early field observations of vertebrate predator-prey systems were not shedding much light on the controversial role of predation. Wildlife biologists maintained that raptors exerted control over rodent pests (e.g. Craighead & Craighead 1956), but not over valued game species. Errington (1946, 1963) introduced the valuable concept of compensatory mortality, but he contended that nearly all prey killed by predators belonged to a 'doomed surplus' which would have died anyway, and concluded that predators have little effect on prey populations. This argument immersed wildlife biologists into "a morass of tortuous verbal logic, a morass from which they are only just now emerging and which would have been quickly and cleanly bridged by the mathematical theory" (Taylor 1984). The generalisation that predators consume a doomed surplus is still widely accepted by ecologists today. However, an increasing number of field studies and predator-removal experiments (e.g. Schnell 1968; Trautman, Frederickson & Carter 1973; Gassaway, Stephenson, Davis, Shepherd & Burris 1983; Sih *et al.* 1985; Angerbjörn 1989; Marcstrom, Engren, Cary & Keith 1989; Newsome *et al.* 1989; Newsome 1990) now show that predation can be a significant and additive mortality factor affecting certain vertebrate prey populations, and may have a particularly devastating impact in sudden relationships (e.g. island introductions) which have not had time to evolve (Elton 1927; Carlquist 1965; Pimm 1987; Ebenhard 1988; Woodroffe & Lawton 1990). It has become clear that the generalisation that predators do not control vertebrate prey is as inappropriate as the generalisation that they do.

Ecologists now use a more succinct terminology and ask whether predators limit or regulate their prey (Boutin 1992; Messier & Crete 1985; Korpimäki 1992). Limiting factors are any factors which affect population growth through increased production or loss of individuals; while regulating factors are limiting factors which behave in a density-dependent fashion (Kidd & Lewis 1987; Sinclair 1989; Messier 1991; Korpimäki 1992). A density-dependent factor may in turn be defined as "any component of the environment whose intensity is correlated with population density and whose action affects survival and reproduction" (Murray 1982). Any factor which is found to be mostly responsible for restraining a prey population is described as the principal limiting factor. But demographic factors do not have to suppress a prey population to be described as limiting. In contrast to predictions of the Lotka-Volterra model, field research on prey cycles has often revealed that predation pressure is not maximal at the peak in prey numbers but rather during the decline phase, and prolonged heavy predation is thought to extend the low phase of the prey cycle and thereby influence its periodicity (Pearson 1966, 1971; Fitzgerald 1977; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). In this context, predation fits the definition of a limiting factor but it cannot be described as regulatory.

University of Pretoria etd – Davies, R A G (1994)



For predators to regulate prey populations around some equilibrium level requires that predation rate be maximal at peak prey densities and minimal at low prey densities (density-dependence). This has become an important criterion in recent predator-prey research (e.g. Erlinge 1987; Kidd & Lewis 1987; Erlinge *et al.* 1988; Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). For predation to be truly regulatory it must also be largely additive, i.e. not matched by some other mortality factor when removed. Of special interest is whether predator-regulated prey equilibria are lower than food-regulated equilibria (Taylor 1984). For cyclic prey populations, predation has often been found to be density-dependent in a delayed fashion (Pearson 1966, 1971; Keith *et al.* 1977; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). Many researchers have reported that food shortage is involved in initiating the decline of cyclic prey from peak densities (Kalela 1971; Tast & Kalela 1971; Henttonen & Järvinen 1981; Oksanen & Oksanen 1981; Laine & Henttonen 1983; Keith *et al.* 1984). Only a couple of studies have indicated that predation pressure may be responsible for actually initiating the declines (Henttonen *et al.* 1987; Trostel *et al.* 1987). But experimental provision of food has not prevented declines (see Akçakaya 1992) and most researchers are now in agreement that the delay or time-lag shown by specialist predators is a crucial element in the pattern of cycles. These time-lags have been attributed to slower rates of reproduction by the predator, and prey refuges such as snow for microtines or thickets for snowshoe hares.

With the resurgence of 'ratio-dependent' predator-prey theory, there has been a closer marriage of theoretical and empirical studies on predation and a clearer explanation of vertebrate population processes. Predator rate of increase and predation rate are now modelled on the ratio of prey to predators (*per capita* resources), rather than absolute prey density. Thus a simple element of interference and sharing between predators is inherent in these new models which are more stable as well as being more plausible for many biological systems. Ratio-dependent theory also solves some of the previous paradoxes of predator-prey models such as enrichment of the lower trophic level (Slobodkin 1992). Akçakaya (1992) used ratio-dependence theory to develop a simple model which adequately explains prey cycling as an interaction between predation and food resources in the presence of a refuge function. This model correctly predicted the periodicity of snowshoe hare cycling and the decline in cycle amplitude towards southern latitudes. This latter tendency is well-known and workers in southern Fennoscandia have now supplied evidence of density-dependent predation by generalist predators which can result in truncated prey peaks or the absence of cycles farther south (Erlinge 1987; Erlinge *et al.* 1988; Korpimäki & Norrdahl 1989b; Korpimäki & Norrdahl 1991; Korpimäki 1992). Greater efficiency of the southern predation response (at preventing major build-ups in prey populations) has been attributed to: reduced prey refuge; the rapid functional response of resident generalist predators subsisting on alternate prey; and the very rapid numeric response of mobile raptors (Korpimäki 1985a; Korpimäki 1992).

Studies of the influence of predation on cyclic prey have been pertinent to observations on non-cyclic but irruptive prey populations. In Australia and New Zealand populations of rabbits and house mice have exhibited 'apparent' cycles which have been characterised by destruction of food resources at peak prey densities and by high predation impact during the low phase (Gibb 1981; Newsome *et al.* 1989; Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992). But these outbreaks have not been regular and the build-up in numbers were attributed to periods of optimal conditions for prey growth, whilst the declines were associated with episodic droughts. For these reasons, this interaction has been best-described as 'environmentally-modulated predation' (Newsome *et al.* 1989). Situations

University of Pretoria etd – Davies, R A G (1994)


where predation is extremely limiting or density-dependent (regulatory) at low prey densities but not at high prey densities have also been observed for large ungulate prey populations in North America (Crête, Taylor & Jordan 1981; Bergerud, Wyett & Snider 1983; Gassaway *et al.* 1983, 1992; Messier & Crête 1984, 1985; Messier 1987, 1989; Van Ballenberghe 1987; Ballard *et al.* 1990). In these circumstances, prey populations are regulated for extended periods by predators after they have been reduced to low density by some other factor. Certain predator removal experiments have demonstrated that predation can be extremely limiting in this way (e.g. Trautman *et al.* 1973; Gassaway *et al* 1983, 1992; Newsome *et al.* 1989; Newsome 1990; Pech *et al.* 1992; see Table 21.1 in Crawley 1992).

Environmentally-modulated predation might be anticipated for rock hyrax populations living in the 'boom and bust' karoo environment. Hyrax irruptions have been reported four times in South Africa and Namibia during the last century (details in Chapter 1: p. 2). There is no indication from these reports that the irruptions were occurring at regular intervals. After the major hyrax decline reported throughout southern Africa which preceded the present study, one might expect that predation impact, especially by specialist black eagles, would be greatest during current low prey densities, but rock hyrax populations have an important analogy to cyclic prey populations in the northern hemisphere - that of a refuge resource which is likely to confer protection at low densities. But unlike snow and microtines, rock crevices are permanent and afford protection to hyrax from nearly all predators. The presence of permanent, effective refuge and the periodic enrichment of hyrax food resources in the vicinity of the refuge habitat by sporadic rainfall events are two characteristics which combine to make this predator-prey system rather unique.

A number of rock hyrax population studies were initiated in response to the alleged agricultural importance of hyrax irruptions. With their readily discernible age classes and a distinct birth-pulse, rock hyrax populations in the Cape are well suited to population modelling. Swart *et al.* (1986) modelled the interaction between rock hyrax and caracals in the Mountain Zebra National Park, and incorporated some elements of ratio-dependence. Their model predicted that caracals merely tracked changes in hyrax density (rather than influencing these changes), and sensitivity analysis suggested that juvenile hyrax mortality had a greater influence on population change than predation (these factors were considered separate). Black eagle predation was set at a very high rate (@307 hyrax pair$^{-1}$ y$^{-1}$) and not allowed to vary for simulations of their model. Fairall *et al.* (1986) constructed a simpler model of the growth of a small rock hyrax population in the Tsitsikama National Park and created equilibrium by means of an increasing death rate factor which was held to represent the limiting influence of shelter on the population. Estimates of carrying capacity were arbitrarily chosen for both models and hyrax mortality was assumed to vary as a simple function of density in relation to carrying capacity. Neither model incorporated a lower trophic level to include the very profound effects of rainfall (via enrichment of food supplies) and drought on hyrax population dynamics (see Chapter 4), but Fairall *et al.* (1986) did simulate population recovery after a catastrophic mortality event. The assumption that hyrax mortality is simply density-dependent and the lack of a lower trophic sub-model to cater for rainfall effects are thought to confer a high degree of artificial stability on both these models.

The prime aim of this chapter is to elucidate what effect black eagles have on hyrax demography. The possible influence of black eagles on hyrax morphology, lifestyle and behaviour is treated elsewhere. In the first part of this chapter all information presented in previous chapters of this thesis is collated in order to assess the immediate

University of Pretoria etd – Davies, R A G (1994)



impact of black eagle predation on rock hyrax during the study period in terms of hyrax standing crop, recruitment and mortality. Comparisons are made with other similar studies of the impact of predation within vertebrate communities. To take these inferences further in the context of the highly changeable Karoo, a specific hyrax population model is evolved in the second part of the chapter. The model is based on accurate measurement of the refuge habitat, and incorporates periodic enrichment of the system through a lower trophic level to yield dynamic estimates of carrying capacity. Hyrax demographic processes are modelled on the ratio between population size and this variable carrying capacity and on rainfall effects, rather than simple density-dependence. The new notion of 'availability-dependent' predation is backed up with evidence from the field. Using long-term climatic data from the Karoo to effectively extend the study period, the model makes predictions which are compared with records of historic hyrax irruptions. The model is used to examine the influence of various aspects of black eagle predation and other factors on rock hyrax demographic processes, and so establish whether hyrax numbers are most influenced by their lower trophic interaction with food supplies or by predation. Consequences of predator control programmes for karoo farmers are forecasted by simulated removal/impedance of predators.

University of Pretoria etd – Davies, R A G (1994)



PART 1

# *THE IMMEDIATE INFLUENCE OF PREDATION BY BLACK EAGLES ON ROCK HYRAX DEMOGRAPHY DURING THE STUDY PERIOD*

## METHODS (part 1)

Keith (1974) provided the following guidelines for evaluating the relative importance of a factor that might affect populations: identify its immediate demographic effect(s), and compare its impact with other factors; describe its interaction with other factors in terms of additive, compensatory or modifying effects; and characterise its action in relation to population density. In this first part of the chapter analyses of hyrax demographic processes during the study period provide the foundation for evolution of a population model in the second part which characterises the long-term action of predation on hyrax population density in the Karoo.

*Immediate demographic effect of predation by black eagles on rock hyrax*

Field data for the study period on rock hyrax demography (Chapter 4), black eagle demography (Chapter 6), prey capture rate by black eagles (Chapter 8), and black eagle diet (Chapters 9 & 10), are provided earlier in this thesis. For methodology see relevant chapters. This part of the chapter is a collation and interpretation of all these data to derive the immediate impact of predation by black eagles on rock hyrax during the period of study in terms of hyrax standing crop, recruitment and mortality. A literature review (Dialog Information Services, Inc.) provided similar case studies of vertebrate predation for comparison.

*Other factors*

The impact of caracals and other generalist predators on different components of rock hyrax populations is assessed from data and literature on the demography and feeding habits of these predators treated in Chapter 7. Inferences on other mortality factors affecting the hyrax population under study (e.g. starvation and disease), and factors affecting recruitment to this population (e.g. conception rates and foetal resorption) are drawn from observations of hyrax population change, from data from the shot sample, and from the literature (see Chapter 4). Predation impact of black eagles on red rock rabbits (and other alternate prey) is derived from data on rabbit demography (see Chapter 5), to enable comparison with black eagle impact on their main prey. Impact of black eagles on domestic livestock was treated in Chapter 11.

University of Pretoria etd – Davies, R A G (1994)



*Interactive effects of demographic factors*

Predation is more likely to remove a random sample of both sick and healthy individuals from a prey population in the case of raptors which rely mainly on surprise tactics in their hunting, than in the case of raptors which actively outfly their prey (Rudebeck 1950, 1951; Kenward 1978a). Black eagles definitely fall into the former category (Chapter 6), but it also seems probable that rock hyrax which are severely food-stressed are more likely to be captured by eagles because they may have to forage farther from shelter (see later). To address the question of whether prey taken by a predator 'would have died anyway' (doomed surplus), is very difficult in the absence of experimental manipulation (Boutin 1992). Black eagles could not be removed in the present study, and the degree of 'compensation' in rock hyrax predation by black eagles could only be explored in a largely speculative way (however, incidental observations of hyrax population change on a farm where all predators except black eagles were actively removed did provide some valuable insights). The age structure of hyrax captured by black eagles in the present field study (Chapter 10) coupled with the amount of age-specific mortality attributable to eagles, did provide some clues as to how many of the rock hyrax captured might have died anyway from old age. But the field study did not provide an indication of how many of the rock hyrax captured by black eagles were dying from starvation or disease. The only literature accessed on compensatory predation by eagles pertained to predation on domestic livestock. But heavy predation of dying lambs by eagles is not very relevant to the black eagle - rock hyrax system, because there is usually an abundance of sickly lambs and because juvenile domestic livestock are close to the maximum size limit of prey taken by eagles. Literature on rock hyrax predation by caracals was accessed to indicate the impact of this predator where black eagles were limited by nest-site availability and vegetation density (details in Chapter 7). The effects of compensatory mortality of hyrax in the absence of predation by black eagles, are further explored in the second part of this chapter when simulating removal of the eagles from the hyrax population model.

University of Pretoria etd – Davies, R A G (1994)



## RESULTS AND DISCUSSION (part 1)

*The impact of predation by black eagles in relation to hyrax standing crop*

Estimates for the number of rock hyrax (in three age classes) alive at the start of each year, dying in the course of the year, and captured by black eagles in the average lower escarpment eagle territory, are presented in Table 42. These data are taken from previous chapters in this thesis (see methods). For the three years when all parameters were comprehensively researched (1988 - 1990), the number of hyrax removed by black eagles from an eagle territory in an average year (117) was equivalent to 11% of the average standing crop of hyrax (1062) at the start of the year, just after the birth pulse. The relative influence of this predation rate on population density depends on the turnover of the hyrax population in terms of annual recruitment and mortality.

### TABLE 42
### ANNUAL ESTIMATES OF PREY AVAILABILITY AND PREY CAPTURED IN AN AVERAGE EAGLE TERRITORY DURING THE STUDY PERIOD

Estimates of hyrax availability, composition and mortality were derived from December counts at colonies in conjunction with group plotting (Chapter 4). Red rock rabbit population estimates were based on midden densities and animal to midden ratios (Chapter 5). The toll taken by eagles of these two prey was derived from information on eagle feeding habits presented in Chapters 8, 9 & 10.

| YEAR | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
|---|---|---|---|---|---|---|
| *hyrax composition:* | | | | | | |
| JUVENILES AT START | | (510) | 428 | 351 | 431 | 199 |
| IMMATURES AT START | | (262) | 208 | 144 | 144 | 262 |
| ADULTS AT START | | (673) | 588 | 405 | 451 | 461 |
| TOTAL AT START | | (1445) | 1224 | 899 | 1025 | 904 |
| *hyrax mortality:* | | | | | | |
| JUVENILES DYING | | (302) | 284 | 207 | 169 | |
| IMMATURES DYING | | (97) | 114 | 40 | 43 | |
| ADULTS DYING | | (250) | 277 | 58 | 91 | |
| TOTAL DYING | | (649) | 675 | 305 | 303 | |
| *impact of predation:* | | | | | | |
| HYRAX KILLED BY EAGLES | (118) | 122 | 136 | 98 | (118) | |
| % STANDING CROP REMOVED | | (8,4) | 11,1 | 10,9 | (11,5) | |
| % EQUIVALENT IN RECRUITMENT | | (24) | 32 | 28 | (27) | |
| % MORTALITY ATTRIBUTABLE TO EAGLES | | (19) | 20 | 32 | (39) | |
| *other prey:* | | | | | | |
| RED ROCK RABBITS AT START | | | | | 441 | |
| RED ROCK RABBITS KILLED BY EAGLES | (35) | 24 | 33 | 49 | (35) | |

University of Pretoria etd – Davies, R A G (1994)



Vertebrate predators normally remove about 15% of vertebrate prey populations. This figure is derived as the average impact for 50 similar investigations of such systems accessed from the literature, but some of these studies refer to predator communities rather than individual species (Table 43). Predation impact is evidently highly variable in vertebrate communities (s.d.=14%; Table 43), and it has to be borne in mind that predation studies are probably less likely to be carried out where predation impact is suspected to be minimal. The studies in Table 43 (consult table for reference numbers) suggest that predation impact is usually high for prey species which can show rapid population turnover, for instance small mammals (e.g. 1, 5, 8, 11, 55, 56) and fish (52). But there was no clear relationship with prey body size. In fact moose (7) and wildebeest (9) were amongst the most heavily preyed upon species. Even carnivores suffered extremely heavy predation in one study (2), but this case could be attributed to cyclicity of a predominant prey species in keeping with the alternative prey hypothesis (Hagen 1952; Lack 1954). Predation impact on cyclic prey is known to be relatively light during the irruptive phase (50), but can be extremely heavy during the decline phase (1). Predation impact by the same predators on the same prey species can vary dramatically with predator-prey ratios on a regional basis (25 vs. 41), and also in relation to the social status of the prey animals (19 vs. 42). Impact also appears to vary with prey vulnerability, for instance raptor communities in North America remove a greater component of mammalian prey populations (4, 11, 13) than avian prey populations (24, 32). Less vulnerable prey species suffer considerably less predation from predators which are concentrating their efforts on more available prey species in the area (5 vs. 43 & 49). Black eagle predation impact on rock hyrax might be expected to be relatively high on the basis that this is a highly specialised predator concentrating on a prey which can be extremely vulnerable. Predation impact is often greatest when specialist predators pursue their prey at low density (e.g. Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Henttonen 1985; Henttonen *et al.* 1987; Korpimäki *et al.* 1991). Also rock hyrax are renowned for their propensity for population increase (Millar 1971; Fourie 1983). It was surprising therefore that the impact recorded in this study was lower than the average recorded for vertebrate systems as represented in Table 43.

*The impact of predation by black eagles on other prey species*

Red rock rabbit midden densities assessed by transect sampling and the accumulation rate of faeces on certain middens indicated that the average lower escarpment eagle territory accommodated approximately 440 red rock rabbits early in 1990 (see Chapter 5). It is estimated that black eagles annually removed an average of 35 rabbits per eagle territory (Table 42). This would imply a predation rate of 8% of the rabbit standing crop. However, incidental observations indicated wide variation in rabbit numbers over the study period (Chapter 5) with a seven-fold increase in sightings between 1987 and 1989. Time-lapse data on rabbit predation in the second half of 1989 provided the closest data on prey capture rate for comparison with the population estimate derived early in 1990, and suggests that predation impact may have been as high as 11% of the standing crop at that time.

Lower predation impact on hyrax than expected, and substantial reliance on red rock rabbits and other alternate prey (Table 34, p. 195) are suggestive that black eagles were hard pressed to catch rock hyrax during the study period. This is supported by the low rate of prey capture observed in the present study (Chapter 8) in comparison with work in the Matobo Hills (Gargett 1990). A likely explanation for this is that after their major population decline in the early 1980's, the rock hyrax in the KRNP were now well protected within the safe confines of their refuge habitat (for predation impact of black eagles on domestic livestock see Chapter 11).

University of Pretoria etd – Davies, R A G (1994)


# TABLE 43

## PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PORTION OF STANDING CROP REMOVED OVER VARYING TIME PERIODS

(numbers in the first column are used for reference from the text)

| Ref. no. | SOURCE | PREDATOR | PREY | PORTION OF STANDING CROP REMOVED | TIME PERIOD |
|---|---|---|---|---|---|
| 1 | Pearson (1966): decline phase | various | California vole | 25 - 88% | (decline) |
| 2 | Korpimaki & Norrdahl (1989a) | mainly raptors | mustelids | 20 - 80% | 1 y |
| 3 | Edminster (1939) | various | ruffed grouse | 40% | 1 y |
| 4 | Craighead & Craighead (1956) | raptors | rabbits | 33 - 47% | fall & winter |
| 5 | Luttich et al. (1970) | red-tailed hawk | Richardson's ground squirrel | 32 - 44% | summer |
| 6 | Linden & Wickman (1983) | Goshawk | Hazel Grouse | 36% | 1 y |
| 7 | Gassaway et al. (1992) | various | moose | 31% | 1 y |
| 8 | Fitzgerald (1977) | ermine | vole | 6 - 54% | 1 y |
| 9 | White (unpubl.) | lion | wildebeest | 28% | 1 y |
| 10 | Keith et al. (1977) | various | snowshoe hare | 12 - 43% | 1 y |
| 11 | Craighead & Craighead (1956) | raptors | meadow mouse | 22 - 26% | fall & winter |
| 12 | Gassaway et al. (1983) | wolves | moose | 13 - 34% | winter |
| 13 | Craighead & Craighead (1956) | raptors | white-footed mice | 22 - 24% | fall & winter |
| 14 | Kenward (1978b) | goshawks | pheasants | 20% | winter |
| 15 | Messier & Crete (1985): low hunting | wolves | moose | 19,3% | 1 y |
| 16 | Whitfield (1985) | raptors | ringed plovers | 19% | winter |
| 17 | Whitfield (1985) | raptors | redshanks | 16 - 20% | winter |
| 18 | Fuller & Keith (1980) | wolves | moose | 15% | 1 y |
| 19 | Jenkins et al. (1964) | various | non-territorial red grouse | 14% | 10 mth |
| 20 | Perrins & Geer (1980) | sparrowhawk | adult tits | 14% | summer |
| 21 | Goransson (1975) | goshawks | pheasants | 10 - 15% | winter |
| 22 | Mills (unpubl.) | lion | zebra | 12% | 1 y |
| 23 | Craighead & Craighead (1956) | raptors | game birds | 5 - 18% | fall & winter |
| 24 | present study | black eagle | rock hyrax | 11% | 1 y |
| 25 | Kruuk (1972a): Ngorogoro | hyenas | adult wildebeest | 11% | 1 y |
| 26 | Fourie (1983): estimated | caracal | rock hyrax | 11% | 1 y |
| 27 | Van Dobben (1952) | cormorants | eels & pike-perch | 10% | breed season |
| 28 | Banfield (1947): outbreak | short-eared owls | voles | 10% | 1 y |
| 29 | Kruuk (1972a): Ngorogoro | hyenas | zebra | 9% | 1 y |
| 30 | Messier & Crete (1985): heavy hunting | wolves | moose | 6 - 11% | 1 y |
| 31 | Korpimaki (1981) | Tengmalm's owl | small mammals | 1 - 15% | 1 y |
| 32 | Craighead & Craighead (1956) | raptors | small birds | 4 - 11% | fall & winter |
| 33 | Picozzi (1978) | Hen Harrier | Red Grouse | 7,4% | 1 y |
| 34 | Ballard et al. (1987): exploited wolves | wolves | moose | 4 - 6% | 1 y |
| 35 | Whitfield (1985) | raptors | turnstones | 4 - 5% | winter |
| 36 | Craighead & Craighead (1956) | raptors | fox squirrel | 4 - 5% | fall & winter |
| 37 | Nellis et al. (1972) | lynx | snowshoe hare | 2 - 6% | winter |
| 38 | Nellis et al. (1972) | lynx | ruffed grouse | 1 - 6% | winter |
| 39 | Messier & Crete (1985): heavy hunting | bears | moose | 1,5 - 5% | 1 y |
| 40 | Kruuk (1972a): Serengeti | hyenas | gazelles | 1,1 - 3,5% | 1 y |
| 41 | Kruuk (1972a): Serengeti | hyenas | adult wildebeest | 1,6 - 2,6% | 1 y |
| 42 | Jenkins et al. (1964) | various | territorial red grouse | 2% | 10 mth |
| 43 | Luttich et al. (1970) | red-tailed hawk | ruffed grouse | 1,5 - 2,4% | summer |
| 44 | Kruuk (1972a): Ngorogoro | hyenas | gazelles | 1,8% | 1 y |
| 45 | Nellis et al. (1972) | lynx | red squirrel | 1 - 2% | winter |
| 46 | Whitfield (1985) | raptors | knots | 0,5 - 1,5% | winter |
| 47 | Blanco & Hiraldo (1991) | red kites | rabbits | 1,2% | breed season |
| 48 | Kruuk (1972a): Serengeti | hyenas | zebra | 0,8 - 1,0% | 1 y |
| 49 | Luttich et al. (1970) | red-tailed hawk | snowshoe hare | 0,7 - 1,2% | summer |
| 50 | Chitty (1938): outbreak | short-eared owls | field voles | 0,05% | 1 y |
| | | | | | |
| 51 | Calaby (1951) | little eagle | rabbits | 2,4% | 10 w |
| 52 | Whoriskey & Fitzgerald (1985) | Avian | Stikkleback | 30% | 2 mth |
| 53 | Southern & Lowe (1982) | Tawny Owl | Bank vole | 25% | 2 mth |
| 54 | Tinbergen (1946) | sparrowhawks | sparrows | 8% | 1 mth |
| 55 | Erlinge et al. (1983) | various | field vole | 12 - 60% | 1 mth |
| 56 | Erlinge et al. (1983) | various | wood mice | 10 - 30% | 1 mth |
| 57 | Raptor Group (1982) | raptors | voles | 0,2% | 1 d |

University of Pretoria etd – Davies, R A G (1994)



*The impact of predation by black eagles in relation to hyrax mortality*

For the years 1988 through to 1990, the number of hyrax dying annually in a lower escarpment eagle territory averaged 428. Predation by black eagles could account for 27,4% of the hyrax that were dying (=117). More than half of the total mortalities were juvenile hyrax, and smaller, generalist predators may have been more involved in these deaths (Chapter 7). The average amount of mortality in vertebrate predator-prey systems that could be attributed to predators was 52% for 20 studies accessed from the literature (Table 44 - consult this table for reference numbers cited in the text), but again this was highly variable (s.d.=26%). Predators were the most important cause of death in studies of large ungulates (57, 58, 61, 62) and in studies of declining, cyclic prey (59, 60). Predators accounted for much greater portions of prey mortality when conditions were good (57) than when conditions were bad (70). Very high losses of hyrax to factors other than eagles in the dry year of 1988 were partly responsible for the relatively low portion of mortality attributable to predation by eagles in the present study. In 1988 eagles accounted for only 20% of hyrax deaths in their territories, but this figure rose to 32% and 39% in 1989 and 1990 respectively, following good rains in 1989. In the two latter years, predation by eagles accounted for most of the adult hyrax dying in their territories (Fig. 95, p. 216). The role of predation by eagles in age-specific mortality was considered in detail in Chapter 10, but it is important to note that other predators are probably more involved in the removal of juvenile hyrax. Black eagles however, exert a high rate of predation on old hyrax, which normally comprise about 16% of hyrax captured (Chapter 10). In the absence of eagles, a component of these would probably die from old age. The degree of such compensatory mortality is likely to vary with circumstance because eagles are more likely to kill surplus elements of hyrax populations such as males and old animals (which may die from other causes) from large vulnerable populations (Chapter 10). Predation is more likely to remove healthy and contributing individuals from a small prey population (additive mortality) where the predator to prey ratio is high (Chapter 10; Kruuk 1972a).

*The impact of predation by black eagles in relation to hyrax recruitment*

Prey vulnerability can vary markedly with life cycle, and the eggs or young of animals may be exposed to a much wider array of predators than the adults. Naive behaviour and small size of juveniles can render them especially vulnerable to predation (Chapter 10). Seventeen studies of predation impact on juvenile elements in prey populations are summarised in Table 45 - these yield an average impact of just over one third of young being removed by predators. Predation evidently has a very dramatic impact on recruitment in certain small mammal (78, 79, 82) and ungulate (80, 81) prey populations. While black eagles accounted for a small proportion of the juvenile hyrax that were dying (Chapter 10), it is enlightening to equate total numbers removed by the eagles with total numbers added each year.

The estimated annual toll of rock hyrax removed from a lower escarpment territory by black eagles for the years 1988 to 1990 (117) was equivalent to 29% of the mean number of juveniles produced at each birth pulse preceding these three years (average no. juveniles = 403; this figure is reduced to 352 if the birth pulse at the end of 1990 is included). Annual recruitment for this period was thus 6% lower than annual mortality and the hyrax population showed an

University of Pretoria etd – Davies, R A G (1994)



## TABLE 44
## PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PROPORTION OF PREY MORTALITY ACCOUNTED FOR BY PREDATORS

(numbers in the first column are referred to from the text)

| Ref. no. | SOURCE | PREDATOR | PREY | % MORTALITY ACCOUNTED FOR | TIME PERIOD |
|---|---|---|---|---|---|
| 58 | Mills (unpubl.) | lion | wildebeest | 93% | wet years |
| 59 | Filonov (1989) | various | roe deer | 91% | 1 y |
| 60 | Trostel et al. (1987) | various | snowshoe hare | 85,1% | 1 y |
| 61 | Keith et al. (1984) | various | snowshoe hare | 80 - 90% | 1 y |
| 62 | Gassaway et al. (1992) | various | moose | 80,5% | 1 y |
| 63 | Jedrzejewski et al. (1992) | mainly wolves | red deer | 80% | 1 y |
| 64 | Filonov (1989) | various | red deer | 65% | 1 y |
| 65 | Smeenk in Brown (1976) | eagles | dik diks | 40 - 60% | 1 y |
| 66 | Eng & Guilliam (1962) | goshawk | ruffed grouse | 50% | winter |
| 67 | Keith et al. (1977) | various | snowshoe hare | 22 - 71% | 1 y |
| 68 | Luttich et al. (1970) | red-tailed hawk | adult Richardson's ground squirrels | 38 - 53% | summer |
| 69 | Nelson & Mech (1981) | wolves | deer | 45% | 1 y |
| 70 | Luttich et al. (1970) | red-tailed hawk | juvenile Richardson's ground squirrels | 37 - 44% | summer |
| 71 | Mills (unpubl.) | lion | wildebeest | 38% | dry years |
| 72 | Nellis et al. (1972) | Canadian lynx | Snowshoe hare | 37% | winter |
| 73 | Tinbergen (1946) | sparrowhawk | small birds | 25 - 50% | season |
| 74 | Hauge & Keith (1981) | wolves | moose calves | 29% | 1 y |
| 75 | Southern (1954) | owls | rodents | 25% | 1 y |
| 76 | Nellis et al. (1972) | lynx | snowshoe hare | 8 - 37% | 1 y |
| 77 | Dumke & Pils (1973) | raptors | pheasant | 20% | 1 y |
| 78 | Jedrzejewski et al. (1992) | mainly wolves | wild boar | 13% | 1 y |

## TABLE 45
## PREDATION IMPACT STUDIES OF VERTEBRATE PREDATORS UPON VERTEBRATE PREY - IN TERMS OF THE PROPORTION OF JUVENILE ELEMENTS REMOVED BY PREDATORS

(numbers in the first column are referred to from the text)

| Ref. no. | SOURCE | PREDATOR | PREY | PORTION REMOVED | TIME PERIOD |
|---|---|---|---|---|---|
| 79 | Erlinge et al. (1983) | various | field vole production | 97% | 1 y |
| 80 | Wood (1980) | various | rabbit juveniles | up to 90% | 1 y |
| 81 | Nelson & Mech (1981) | wolves | deer fawns | 71% | fall - winter |
| 82 | White (unpubl.) | lion | wildebeest recruitment | 71% | 1 y |
| 83 | Myers & Schneider (1964) | various | rabbit juveniles | 70% | 1 y |
| 84 | various in Boutin (1992) | bears | moose calves | 34 - 52% | 1 y |
| 85 | Scott & Klimstra (1955) | red fox | bobwhite quail nests | 41,3% | 1 y |
| 86 | Maclean et al. (1974) | weasel | lemming nests | 35% | winter |
| 87 | Murie (1992) | badgers | Columbian ground squirrels juveniles | 25% | 1 y |
| 88 | Hauge & Keith (1981) | wolves | moose calves | 21% | 1 y |
| 89 | Dunn (1977) | weasel | tit nests | 21 % (up to 51%) | 1 y |
| 90 | Jarvinen (1985) | mustelids | passerine nests in holes | 20% | 1 y |
| 91 | Perrins & Geer (1980) | sparrowhawk | great tit recruitment | 18 - 34% | 1 y |
| 92 | Perrins & Geer (1980) | sparrowhawk | blue tit recruitment | 18 - 27% | 1 y |
| 93 | various in Boutin (1992) | wolves | moose calves | 1 - 18% | 1 y |
| 94 | Sherman (1981) | badgers | Belding's ground squirrel juveniles | 8% | 1 y |
| 95 | Liberg (1984) | Domestic cat | Common rabbit production | 4% | 1 y |
| 96 | Lloyd (1976) | raptors | pheasant poults | 0,25% | 1 y |

University of Pretoria etd – Davies, R A G (1994)


overall decline of 26% between November 1987 and November 1990 (some of this decline must be attributed to the extremely poor recruitment at the end of 1990). The highest annual toll taken by black eagles in the present study (136 per territory in 1988) was equivalent to 68% of the smallest hyrax birth pulse (199 per territory in 1990). Annual predation rates of hyrax by black eagles recorded for the Matobo Hills by Gargett (1990), are much greater than the minimum hyrax birth-pulse recorded for an average eagle territory in the present study. Predation by black eagles evidently has the capacity to be a major restraining influence on hyrax population growth. By slowing the rate of increase of the hyrax population, predation by black eagles can be described as a limiting factor (Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). Without modelling, it is difficult to predict the precise influence of such a restraint on population density, but in the event-driven karoo situation any factor which slows hyrax population growth during enrichment should help alleviate destruction of food resources in subsequent droughts. The field data indicates that, unlike sympatric generalist predators, specialist black eagles continue to exert such an influence (albeit reduced) even when small hyrax populations are well protected within their refuge habitat.

*The impact of predation by generalist predators on rock hyrax during the study period*

Caracals in the KRNP probably outnumber black eagles by a factor of three under normal circumstances, and may consume more than six times as much food (Chapter 7). Yet scat analyses did not indicate that caracals were an important predator of rock hyrax in the early part of the present field study. It is likely that some hyrax were being captured by caracals during the study period, but this remained undetected by the methods employed. Hyrax have comprised a significant portion of caracal diet previously in the KRNP and in other areas, and it is calculated that caracals have the potential to remove approximately 400 hyrax annually from an eagle territory under more usual conditions of hyrax availability (see Chapter 7). The functional and numeric response of caracals should enable this predator to have a much greater impact on surplus rock hyrax than black eagles, when the hyrax population exceeds the carrying capacity of its refuge habitat. Other predators of large hyrax which may have an impact on populations elsewhere in Africa were not sufficiently abundant in the KRNP to have a significant influence on hyrax demography. For more detail on the potential impact of caracals on rock hyrax see Chapter 7.

In an average year during the study period, about 220 (55%) of the 403 juvenile hyrax born in an eagle territory died in their first year. This juvenile mortality has been shown to be highly variable (Chapter 4) and of great importance to hyrax population dynamics (Fourie 1983; Swart *et al.* 1986). Black eagles showed a low preference rating for juveniles in their diet, presumably because of low profitability of such small prey items (Chapter 10). Caracals are larger predators and may exhibit similar prey choice but this has not yet been investigated. In addition to caracals and black eagles, juvenile hyrax are exposed to a wide array of smaller, generalist predators such as Cape wildcats, various raptors and Cape cobras. The impact of the latter on the rock hyrax study population was not comprehensively researched in the present study, but it is roughly estimated that all predators in the KRNP have the potential to account for 40% of the juvenile mortality (Chapter 7). Such an impact may have an important bearing on rock hyrax population change. Predation and juvenile mortality cannot be divorced as separate demographic factors. Observations on the farm Montana, near Victoria West (140km north-east of the KRNP) suggest that removal of generalist predators may lead to very rapid hyrax population growth. In 1984, an irruption of hyrax on

University of Pretoria etd – Davies, R A G (1994)



this farm forced the landowner to move his livestock elsewhere. Shortly afterwards most of the hyrax disappeared in synchrony with a widespread decline during the drought. I revisited the farm in 1990 and learned that the hyrax population had already nearly recovered to the population level experienced prior to the major decline (J.H. Swiegers pers. comm.). Unfortunately this farm was not monitored as a control because black eagles were resident and not persecuted. A second pair of eagles had colonised the farm in the interim. Carnivores however (caracals, Cape wildcats, black-backed jackals, Cape fox), had been heavily persecuted (details in Chapter 11: p. 230-231), and this was considered to be the major difference between the farm Montana and the study area in the KRNP where the hyrax population had shown no obvious recovery between 1986 and 1990. Prolonged suppression of prey populations at low density by a healthy complement of predators has been demonstrated elsewhere (Gibb 1981; Gassaway *et al.* 1983, 1992; Van Ballenberghe 1987; Newsome *et al.* 1989; Ballard *et al.* 1990; Newsome 1990; Sinclair *et al.* 1990; Pech *et al.* 1992). Heavy predation of juveniles in a prolific prey species may be necessary for this effect.

*The influence of non-predatory mortality on the hyrax population*

Considerable numbers of hyrax in the study area were evidently dying of causes other than predation by eagles during 1988. Other predators may have been involved in these removals but analyses of scats collected mainly in 1987 did not implicate caracals. It seems likely that many of the hyrax were dying of drought-related causes such as starvation and disease. But very little evidence of such non-predatory mortality could be found, possibly because dying hyrax were either removed by scavengers or they died concealed in crevices. With heavy predation on old hyrax by black eagles and possibly caracals, it is unlikely that a significant number of hyrax reach their full life-expectancy and die of old age. Dental attrition from age eight years onwards can be expected to affect body condition deleteriously and render these animals more vulnerable to predators.

One adult hyrax was observed on the upper escarpment in 1989 which showed behaviour that may have been symptomatic of rabies (salivation, poor vision and coordination, and no fear of humans). A farmer in the area reported many such cases when hyrax were at high population density in the mid 1970's (D. Shearing pers. comm.). Rock hyrax are 'close-contact' social animals, and would be very susceptible to a disease epidemic, especially when high densities of animals are stressed by drought. The spread of disease through hyrax populations may be significantly hampered however, by removal of sickly individuals by predators. Hyrax populations have been known to be affected by outbreaks of bubonic plague (Kingdon 1971) and sarcoptic mange (Hoeck 1982); and an acid-fast bacillus which causes pulmonary tuberculosis was isolated from lungs of hyrax collected in the New Bethesda region (Wagner, Buchanan, Bokkenheuser & Leviseur 1958; Wagner & Bokkenheuser 1961). This raises the speculation that the major population declines observed in the early 1980's may have been caused by disease. However, researchers were censusing hyrax at the time of the decline in the KRNP and did not observe any diseased individuals (N. Fairall pers. comm.). It does seem likely that disease might be involved in hyrax population declines, but it is probably encouraged by other circumstances such as high densities and drought. Major declines of springbok in 1984 on a farm at Victoria West (140km north east of the KRNP) were attributed to a lack of fermentable carbohydrate in the vegetation (Davies 1985), and it is considered most likely that the synchronous hyrax decline was also associated with such food stress.

University of Pretoria etd – Davies, R A G (1994)



At high densities, agonistic encounters between hyrax may also lead to deaths. Wounds inflicted by fighting amongst males can become heavily infested with ixodid ticks, and these animals sometimes die of secondary bacterial infection (Fourie 1983). Incidence of major fractures amongst hyrax skeletal material collected beneath eagle nests suggests that some hyrax may also die as a result of falls and other accidents. Heavy parasite burdens are suspected to cause some hyrax mortalities but this has not yet been confirmed by haematological study of wild animals (Fourie 1983). Hyrax parasite burdens become heavier during periods of good rains (Fourie 1983) - major population increases of hyrax recorded at such times (Chapter 4) do not indicate that heavier parasite loads cause any significant mortality amongst hyrax. Juvenile hyrax appear to be the most susceptible to non-predatory mortality. Fourie (1983) ascribes high mortality of juveniles to heavy parasite burdens; low fat reserves; low thermolability; greater susceptibility to disease; and a reluctance to forage away from natal colonies. These characteristics should indeed render juveniles less adept at coping with food stress during drought, but juveniles were observed to accompany adults on group foraging bouts away from colonies in the present study (Chapter 4).

*The influence of variable recruitment on the hyrax population*

The rate of addition of individuals to the hyrax study population between 1987 and 1990, in terms of mean litter size and pregnancy rate, was very similar to that recorded in other studies of rock hyrax populations in the Karoo (see Chapter 4). It was calculated that in a lower escarpment eagle territory recruitment over the entire study period averaged 352 juveniles per birth pulse (these comprised about 35% of the post birth pulse population). But this recruitment showed considerable annual variation in keeping with other studies (Millar 1971). Three principal factors are involved in this variability: ovulation rates; the incidence of precocious puberty in females; and the incidence of pre-natal mortality (Millar 1971; Fourie 1983). Millar (1971) showed that in good conditions ovulation rates can be considerably higher, and up to 33% of 4-5mth old female hyrax may conceive. These observations were offered as an explanation for the sudden population increases attributed to rock hyrax in the Cape. In less favourable conditions precocious puberty of females is negligible (Fourie 1983) or absent (Steyn 1980), and low ovulation rates result in small litter sizes (Millar 1971; Fourie 1983). Conception rates (in April) are probably most influenced by the amount of preceding summer rainfall (see Chapter 4). After conception in April some of the embryos or foetuses may be aborted or resorbed. Millar (1971) found foetal loss in up to 24% of litters in dry karoo areas (up to 10% foetuses lost), while Fourie (1983) noted heavier foetal loss among older females. Comparisons of reproductive data gathered from females shot in October with the estimated number of births in November were highly suggestive of late pre-natal mortality in 1990 (pages 52 & 62): the number of juveniles counted in December 1989 were only 1% less than predicted from the reproductive data (assuming no neo-natal mortality); whereas the number of juveniles counted in December 1990 were 64% less than expected. Fourie (1983) observed a significant correlation between the extent of pre-natal loss and rainfall during the gestation period (April - November). November rains explained 84% of the variation in hyrax recruitment in the present study (p. 49). Such rains are presumably important to the onset of lactation. But in keeping with Fourie (1983), strongest correlations were obtained between recruitment and rainfall over the entire gestation period from April to November (Figure 105).

University of Pretoria etd – Davies, R A G (1994)



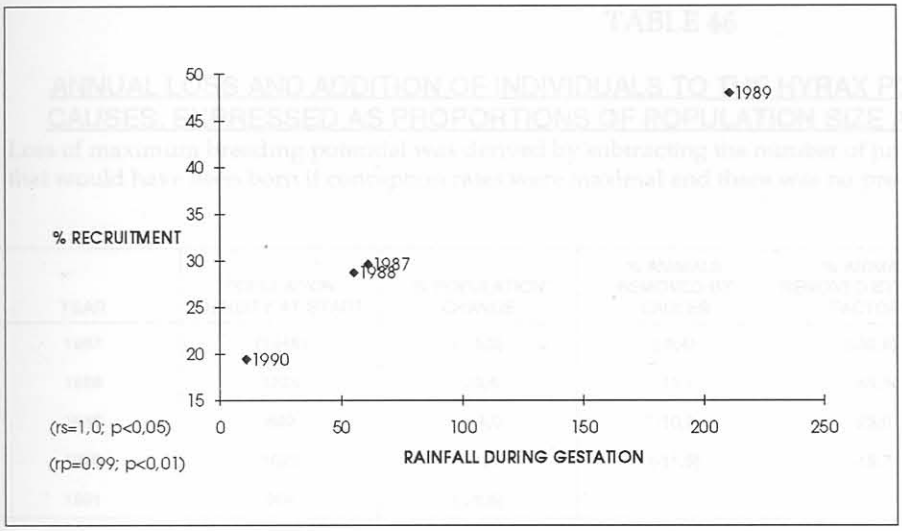



**Figure 105.** The relationship between hyrax recruitment (no. juveniles at a particular birth pulse compared with total population size at the start of the preceding year) and the amount of rain falling during the gestation period.

So the addition of individuals to rock hyrax populations varies dramatically with conception rates (influenced by preceding summer rains) and pre-natal mortality (influenced by rains during gestation). Alternating periods of enrichment and drought, so characteristic of the Karoo, are certain to lead to a changeable recruitment and a highly variable population structure. Population growth can be expected when favourable conditions lead to large birth pulses which may exceed the immediate capacity of local predation. The number of juveniles produced and the number of these which survive their first year are important factors involved in rock hyrax population change, because of their great variability and because of the magnitude of the juvenile population component.

*Inter-annual variation of demographic factors affecting the hyrax population during the study period*

Accurate hyrax census data were only obtained for the four birth pulses between November 1987 and November 1990, but inferences could be made on hyrax population size at the end of 1986 from incidental observations of decline. Some data were gathered in November 1991 but were not reliable. This yielded only 5 data points and four interims for most inter-annual comparisons of demographic factors affecting the hyrax population during the study period. Despite this small sample size, such comparisons may provide a valuable insight to the factors which were most involved in hyrax population change. This can be considered as a simple key-factor analysis (Varley & Gradwell 1960). Estimates of population change in each year of study, mortality to eagles, mortality to other factors, and recruitment, all expressed as a percentage of the population density at the start of respective years are given in Table 46. Trends emerging from correlation analyses performed on these data are given in Table 47. Only two relationships emerged as statistically significant for the appropriate Spearman's rank correlation test. Pearson's correlation coefficients as listed are not suited for testing the significance of relationships on such limited data, but they do give a more appropriate indication of the relative strength of co-relationships. Correlations between demographic factors and population change can be used to suggest which factors are limiting, and limiting factors can be considered regulatory if they are shown to be density-dependent (see earlier). For comparison of recruitment with mortality factors in this way, recruitment should be considered as loss of maximum breeding potential (Clutton-Brock, Major & Guinness 1985; Messier 1991). Loss of breeding potential was derived as the difference between the number of juvenile hyrax born and the number that would have been born if conception rates were maximal and pre-natal mortalities minimal.

University of Pretoria etd – Davies, R A G (1994)



## TABLE 46

### ANNUAL LOSS AND ADDITION OF INDIVIDUALS TO THE HYRAX POPULATION DUE TO VARIOUS CAUSES, EXPRESSED AS PROPORTIONS OF POPULATION SIZE AT THE START OF EACH YEAR

Loss of maximum breeding potential was derived by subtracting the number of juveniles born from the maximum number that would have been born if conception rates were maximal and there was no pre-natal mortality (see text)

| YEAR | POPULATION DENSITY AT START | % POPULATION CHANGE | % ANIMALS REMOVED BY EAGLES | % ANIMALS REMOVED BY OTHER FACTORS | % ADDITIONS AT THE END OF THE YEAR | % LOSS OF MAXIMUM BREEDING POTENTIAL |
|---|---|---|---|---|---|---|
| 1987 | (1445) | (-15,3) | (-8,4) | (-36,5) | (+29,6) | (-63,4) |
| 1988 | 1224 | -26,6 | -11,1 | -44,1 | +28,7 | -56,5 |
| 1989 | 899 | +14,0 | -10,9 | -23,0 | +47,9 | -50,7 |
| 1990 | 1025 | -11,8 | (-11,5) | -19,7 | +19,4 | -81,3 |
| 1991 | 904 | (-26,6) | | | | |

## TABLE 47

### KEY-FACTORS ANALYSIS PERFORMED ON THE INTER-ANNUAL VARIATION OF CERTAIN FACTORS INVOLVED WITH HYRAX DEMOGRAPHY

Demographic values used in this analysis were expressed as proportions of population size at the start of the year(most are listed in Table 46). See Table 46 and text for an explanation of the loss in breeding potential. Spearman's rank correlation is the only appropriate test for the significance of relationships based on such limited data sets (n=4 intervals), but Pearson's correlation coefficients are also presented because these give a better indication of the amplitude of the correlation.

| VARIABLES | | Pearson's correlation | Spearman's correlation |
|---|---|---|---|
| population growth | total mortality | r=-0,72; p=0,27 | n.s. |
| population growth | non-eagle mortality | r=-0,71; p=0,29 | n.s. |
| population growth | loss of breeding potential | r=-0,33; p=0,68 | n.s. |
| population growth | black eagle predation | r=-0,12; p=0,88 | n.s. |
| population growth | population density | r=-0,70; p=0,30 | n.s. |
| population density | black eagle predation | r=-0,80; p=0,21 | n.s. |
| population density | non-eagle mortality | r=0,73; p=0,27 | n.s. |
| population density | loss of breeding potential | r=0,05; p=0,95 | n.s. |
| loss of breeding potential | preceding summer rain | r=0,97; p=0,03 | n.s. |
| loss of breeding potential | total annual rain | r=-0,84; p=0,16 | r=1,0; p<0,05 |
| loss of breeding potential | gestation rain | r=-0,78; p=0,22 | n.s. |
| recruitment | gestation rain | r=0,99; p<0,01 | r=1,0; p<0,05 |
| recruitment | total annual rain | r=0,90; p=0,10 | n.s. |
| non-eagle mortality | preceding summer rain | r=-0,63; p=0,30 | n.s. |

University of Pretoria etd – Davies, R A G (1994)



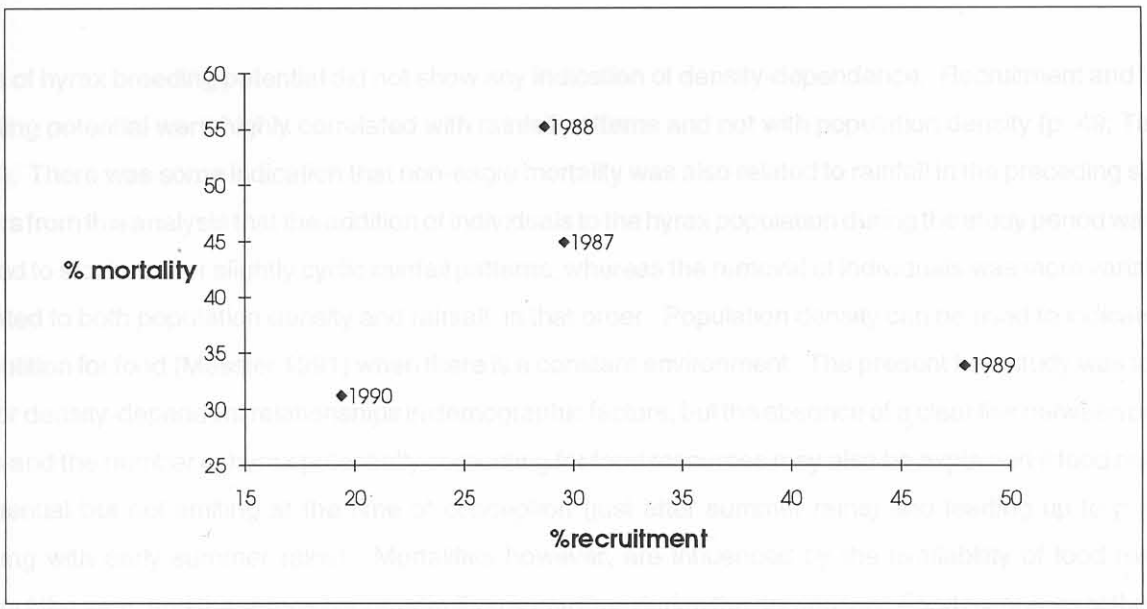



**Figure 106.** Annual plots of mortality and recruitment affecting the hyrax population for the four years of intensive field study. Mortality is calculated as the proportion of the starting population that dies in the following year. Recruitment is calculated as the proportion of the starting population that is added at the end of the year.

Hyrax population change during the study period showed stronger correlations with total mortality and non-eagle mortality than with the loss of breeding potential (Table 47). If recruitment is plotted against mortality for the four years of intensive study (Figure 106), it is relevant to note that the year of greatest population growth (1989) experienced minimal mortality and maximal recruitment, whereas the year of greatest decline (1988) experienced maximal mortality but recruitment was not below average. Numbers removed from the hyrax population during the study period showed more variation than numbers added, and population changes correlated more with the former than the latter (Table 47). Population change in rock hyrax is clearly the combined product of variable mortality and variable recruitment. Although birth pulses did vary dramatically during the study, these were not more responsible for the observed population changes than variation in mortality. There was an overall decline in hyrax numbers during this study - a different result from this analysis may have resulted had the study been conducted during a growth phase for the hyrax population. The involvement of variable additions and variable removals in hyrax population change through alternating growth and decline phases is explored by modelling in the second part of this chapter.

There was no suggestion of any statistical trend linking population growth with predation rate by black eagles. A slight trend between population growth and population density (Table 47) suggested some density-dependent factor/s may have been operating. Non-eagle mortality was the main factor which might have behaved in this manner during the study period. Predation rate by black eagles was apparently negatively correlated with density, but this trend could be entirely attributed to 1987 data when population density was not accurately determined. Black eagles actually captured more hyrax in 1988 (Chapter 8) when the prey population was larger than in subsequent years, but predation rate was remarkably consistent at 11% for the three years when the relevant parameters were well known.

University of Pretoria etd – Davies, R A G (1994)


The loss of hyrax breeding potential did not show any indication of density-dependence. Recruitment and the loss of breeding potential were highly correlated with rainfall patterns and not with population density (p. 49; Table 47; Fig. 106). There was some indication that non-eagle mortality was also related to rainfall in the preceding summer. It appears from this analysis that the addition of individuals to the hyrax population during the study period was highly correlated to stochastic or slightly cyclic rainfall patterns, whereas the removal of individuals was more variable and was related to both population density and rainfall, in that order. Population density can be used to indicate levels of competition for food (Messier 1991) when there is a constant environment. The present field study was too short to look for density-dependent relationships in demographic factors, but the absence of a clear link between breeding success and the number of hyrax potentially competing for food resources may also be explained if food resources are influential but not limiting at the time of conception (just after summer rains) and leading up to parturition (coinciding with early summer rains). Mortalities however, are influenced by the availability of food resources throughout the year, and these may become limiting some time during the dry season. Food resources at this critical period would presumably determine the carrying capacity in the vicinity of the refuge habitat to support hyrax. When numbers exceed this carrying capacity they should be more vulnerable to predation, and if predators are not able to remove the surplus, more susceptible to starvation also.

It is more sensible to expect mortality and predation of rock hyrax to vary with this excess or surplus, rather than as a simple function of density. Large populations of hyrax may be comfortably supported by ample food resources within their refuge habitat after good rains. It is clear that much of the variation in rock hyrax population density in the arid Karoo can be attributed to the short- or long-term influence of rainfall on the vegetation resources. Good rains maximise population growth by leading to both increased recruitment and reduced mortality. Droughts have the opposite effect, especially at high population density. Alternating wet and dry periods have the effect of destabilising hyrax numbers in the Karoo.

Predation by black eagles had the effect of limiting hyrax population growth but did not behave in a density-dependent manner during the present field study. Although black eagles are potentially capable of much higher prey capture rates than observed during the present study, territorial behaviour is strong in this species (Chapter 6) and limits the response that this predator might show to changes in prey density. However Gargett has recently (1992 unpubl.) provided evidence of surprisingly dramatic change in the number of territories maintained by black eagles in the Matobo Hills. If hyrax predation by black eagles is not density-dependent over the long-term, then current theory on predator-prey relationships would hold that such predation could not be regulatory (Kidd & Lewis 1987; Sinclair 1989; Messier 1991; Boutin 1992; Korpimäki 1992). But in the context of the highly variable, 'event-driven' karoo environment, any demographic factor which acts as a consistent 'hand-brake' on population growth may help prevent imbalance arising between prolific species such as hyrax and their changeable food resources. In the absence of experimental manipulation, the exact influence of such a factor can best be explored by population modelling.

University of Pretoria etd – Davies, R A G (1994)



PART 2

# *THEORETICAL PREDICTIONS ON THE LONG-TERM ACTION OF PREDATION BY BLACK EAGLES ON ROCK HYRAX POPULATION DENSITY IN THE KAROO*

## METHODS (part 2)

### FORMULATION OF THE HYRAX POPULATION MODEL -

*Population composition and age-specific rates of mortality and fecundity*

A system dynamics model (Forrester 1968) was formulated for the hyrax population using the 13 annual age classes as recognised by Fourie (1983). Modelling the population to the resolution of these age classes was favoured over simpler versions because processes could then be based on sound biological data, and because recruitment can be expected to vary as the mature female component in the population structure varies. Initial composition of these age classes for males and females was derived from a spreadsheet model (MICROSOFT EXCEL version 4.0) which satisfied most observations of the hyrax population during the period of study (see Chapter 10: Fig. 92, p. 214; Table 36, p. 213), and which was stable over time. On account of the dramatic influence of rainfall on hyrax population structure (Chapters 4 & 10), such stability is strictly only representative of a population in an homogenous environment. However, this structure provided a useful point of departure for further modelling because it represented mediocre conditions when the hyrax population was neither increasing nor declining.

Minima and maxima rates of age-specific mortality and fecundity (pregnancy and litter size) were then needed in order to simulate population change under best conditions (small populations, well protected in the refuge habitat, after good rains) and worst conditions (large populations in an overcrowded refuge habitat during drought). These were derived from the present study (Chapter 4) and from other similar investigations (Millar 1971; Fourie 1983; Fairall *et al.* 1986). Some of the age-specific parameters had to be manipulated in the spreadsheet model in order to yield overall results on adult/immature mortality etc. which conformed to counts at colonies which were cruder (in terms of age classes), but were considered to be more reliable than the life table calculations performed on limited samples. The values used are given in Appendix 6. All further modelling was performed using TURBO PASCAL version 7.0 (Borland International Inc.). A complete print-out of the population model referred to in this chapter is supplied in Appendix 10.

University of Pretoria etd – Davies, R A G (1994)


*Carrying capacity in a standard year*

Actual age-specific rates of mortality and fecundity used by the model in a given year were derived (see next section) from the ratio of P:K, where P equals hyrax population size within a black eagle territory after the birth pulse; and K equals the number of hyrax that can comfortably be accommodated by food resources within the 'safe feeding area' as determined by rocky habitat in the territory. Behavioural observations and vegetation zones (Chapter 4: p. 56-57) indicated that hyrax foraged up to 15m from rocks in the KRNP, so the total 'safe feeding areas' in four neighbouring black eagle territories were determined by 'buffering' all rock outcrops on the geographical information system (ARCINFO) by a radius of 15m. Safe feeding area averaged 538ha (s.d.=24ha) and was the least variable habitat parameter across four eagle territories (but solid rock outcrops occupied 33% of this, leaving only 358ha available for normal plant growth). The carrying capacity of this area for rock hyrax in a standard year was calculated using mean group size for rock hyrax (=16,2: p. 46) and the average area over which individual groups ranged (derived as 4,8ha from Fig. 28, p. 53, for a group of 16,2 hyrax). Not all of the safe feeding area would be suitable for hyrax, but some flexibility in group size is also to be expected. It was concluded that the safe feeding area in an average eagle territory could comfortably accommodate 112 hyrax groups or 1816 individuals under conditions of average rainfall and food supplies (indicating that hyrax densities during the study period were at nearly 60% of this saturation density). Hereon, normal conditions refer to years of average rainfall and average plant production.

*Interpolating mortality and fecundity on P:K ratio*

A fundamental assumption of the model is that hyrax mortality is raised and fecundity is lowered when P exceeds K, whereas the reverse situation engages when P is lower than K. Actual values for age-specific mortality and fecundity were chosen in a given year by linear interpolation (between average and extreme values) based on the discrepancy between P and K. Detailed field data are not yet available on this relationship so a simple linear function was assumed. The discrepancy between P and K necessary to invoke the maximal or minimal rates of mortality and fecundity presented in Appendix 6 is explored later in the modelling - a factor of 3,5 was chosen for standard runs of the model. This is also based to some degree on field data: very heavy mortality and lowered fecundity resulted in a four-fold decline in the hyrax population in the KRNP during the early 1980's (Fairall 1991, *in litt.*), and it was assumed that the hyrax must have exceeded the carrying capacity of their habitat by about four times in order to invoke this decline. So predation is handled in a ratio-dependent manner in the present model, but the predation response is (unconventionally) dependent on the ratio between hyrax and their food resources rather than the ratio between predators and prey. Modelling mortality and fecundity in this way accounts for the way in which food-stress, crowding (and disease transmission), and vulnerability to predation can be expected to vary. It also accommodates for compensatory effects in recruitment resulting from heavy predation. Data in the first part of this chapter suggested that the addition of individuals to the hyrax population was primarily related to rainfall patterns and not population density. This may be because the study was carried out during relatively low hyrax population densities. Nevertheless, accommodation is made in the population model to compare recruitment modelled on rainfall with recruitment modelled on P:K ratio. That hyrax mortality should be high when P far exceeds K seems intuitive, but this fundamental assumption of the model is also based on a few lines of field evidence with regard to predation.

University of Pretoria etd – Davies, R A G (1994)



During the present study, black eagle predation and other mortalities of hyrax were highest in the dry year of 1988 and lowest in the wet years of 1989 and 1990 (Chapters 4 & 8). There was also limited indication that hyrax remained closer to shelter in good conditions (Chapter 4) and that the delivery rate of rock hyrax prey to black eagle nests declined shortly after good rains (Chapter 8). In the Matobo Hills, black eagle breeding success improved from wet years to dry years and declined from dry years to wet years for 23 of the 27 years monitored (see Fig. 107: data given in Gargett 1990, referred to by Allan 1988). The four years when this pattern was not evident occurred after the major hyrax decline in the early 1980's (V. Gargett *in litt.*; R. Barry pers. comm.). Breeding success in raptors is normally related to prey availability (Newton 1979). Bounty records for the Cape Province show that more rock hyrax were destroyed (probably shot) during the dry year of 1949 than in the preceding wet years, suggesting that hyrax mortality due to human predation also increases during drought (P. Norton *in litt.;* see Fig. 108) . Many farmers report that hyrax emerge from rocky outcrops and range farther to feed as conditions become drier (pers. rec.). The fore-going rationale is similar to that proposed by Jones (1979) in a simple model of prey populations (pertaining to vertebrates) where different components of the population are exposed to different rates of predation.

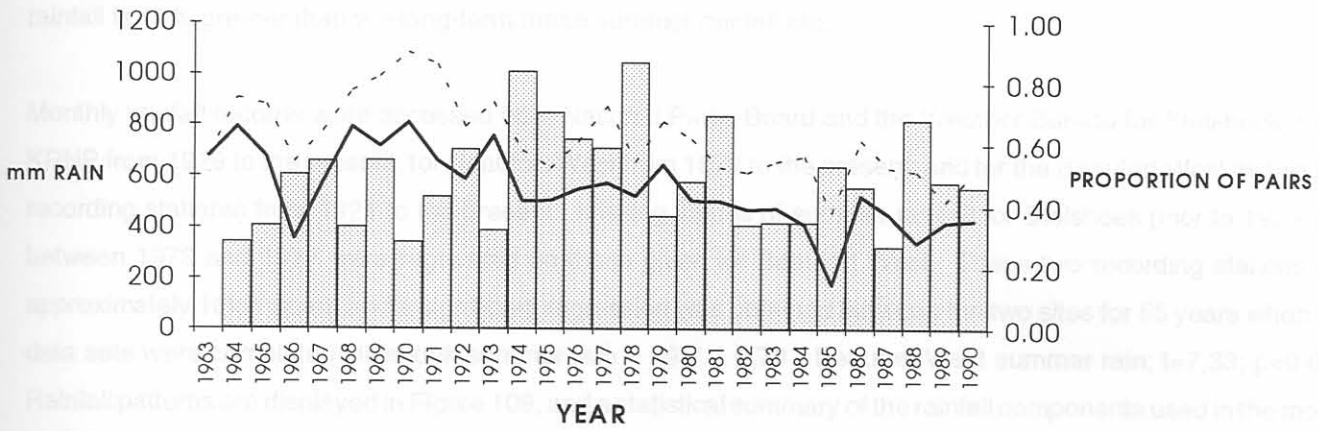



**Figure 107.** Summer rainfall patterns in the Matobo Hills, Zimbabwe, and concordant change in the effort and success of black eagle breeding attempts monitored by Gargett (1990: Tables 1 & 34) & Banfield (*in litt.*). For most of Gargett's study, eagle breeding success improved as rainfall declined and dropped off as rainfall improved (see text). This is thought to reflect changes in hyrax vulnerability and the data are shown here to support rationale adopted in the present hyrax model.

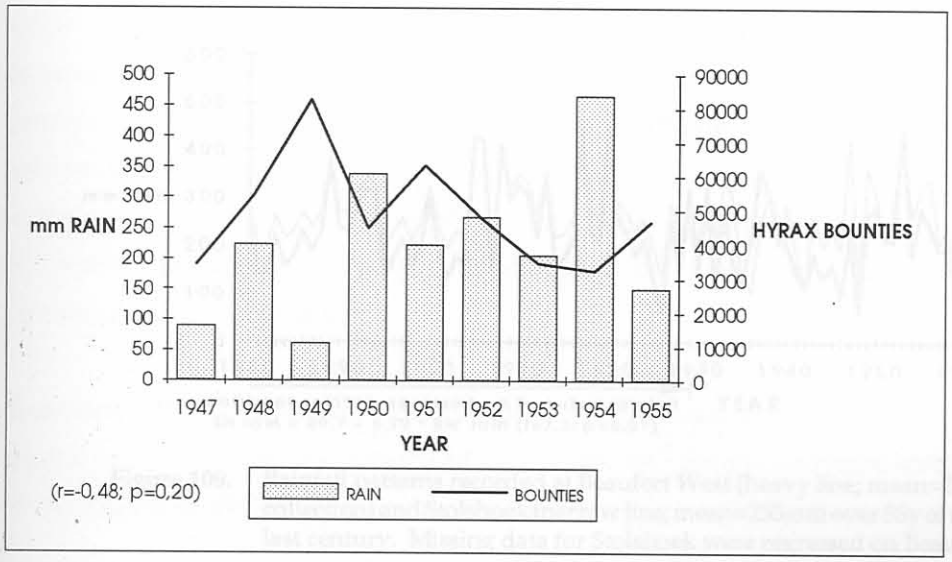



**Fig. 108.** Bounties paid out for the destruction of hyrax in the Cape Province between 1947 and 1955, and rainfall patterns over the same period (from data records of CDNEC - Norton *in litt.*). Beaufort West hyrax bounties reflected a similar trend.

University of Pretoria etd – Davies, R A G (1994)



*A dynamic measure of carrying capacity*

Hyrax population processes were also modelled on the relationship of P to K in previous theoretical investigations (Fairall *et al.* 1986; Swart *et al.* 1986), but K was not based on measurement of rocky habitat in those studies. The present model departs further from these studies by introducing the concept of a dynamic value for K which can take into account the effects of enrichment of the lower trophic level: while the safe feeding area in an eagle territory is a relatively permanent feature determined by the distribution of rocks, the number of hyrax that it can safely support will be greater than standard K in years of good rainfall, and less than standard K during drought. Departure of K from standard K in years of varying rainfall should primarily relate to variation in plant production (hyrax food supply). Extensive analyses of the relationship between rainfall and plant production in arid and semi-arid range-lands by Le Houérou, Bingham & Skerbek (1988) have revealed that variability (measured as the coefficient of variation: $\sigma / \bar{x}$) in plant production on these lands is 1,5 times greater than variability in rainfall. Thus, if the standard deviation of annual rainfall is 10% larger than the mean value, then the standard deviation of annual plant production will be 15% larger than its respective mean. In this model it is assumed that K will be 15% greater than standard K when summer rainfall is 10% greater than the long-term mean summer rainfall etc..

Monthly rainfall records were accessed from National Parks Board and the Weather Bureau for Stolshoek in the KRNP from 1929 to the present; for Beaufort West from 1879 to the present; and for the Beaufort West district (32 recording stations) from 1921 to the present. Missing values of summer rainfall for Stolshoek prior to 1929 and between 1973 and 1977 were regressed on those given for Beaufort West. These two recording stations are approximately 10km apart, and a significant regression was obtained between the two sites for 55 years when the data sets were complete (Stolshoek summer rain = 89,7 + 0,79 * Beaufort West summer rain; t=7,33; p<0,01). Rainfall patterns are displayed in Figure 109, and a statistical summary of the rainfall components used in the model is given in Appendix 7. For most runs of the model, Beaufort West rainfall data are used because of the long history of raw data collection.

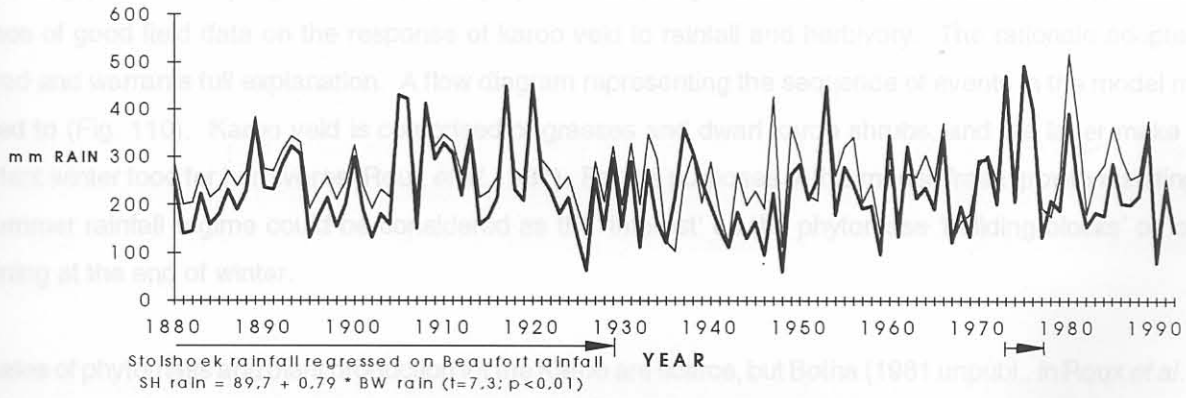



**Figure 109.** Rainfall patterns recorded at Beaufort West (heavy line; mean=212mm over 55y of raw data collection) and Stolshoek (narrow line; mean=255mm over 55y of raw data collection) over the last century. Missing data for Stolshoek were regressed on Beaufort West data as shown.

University of Pretoria etd – Davies, R A G (1994)



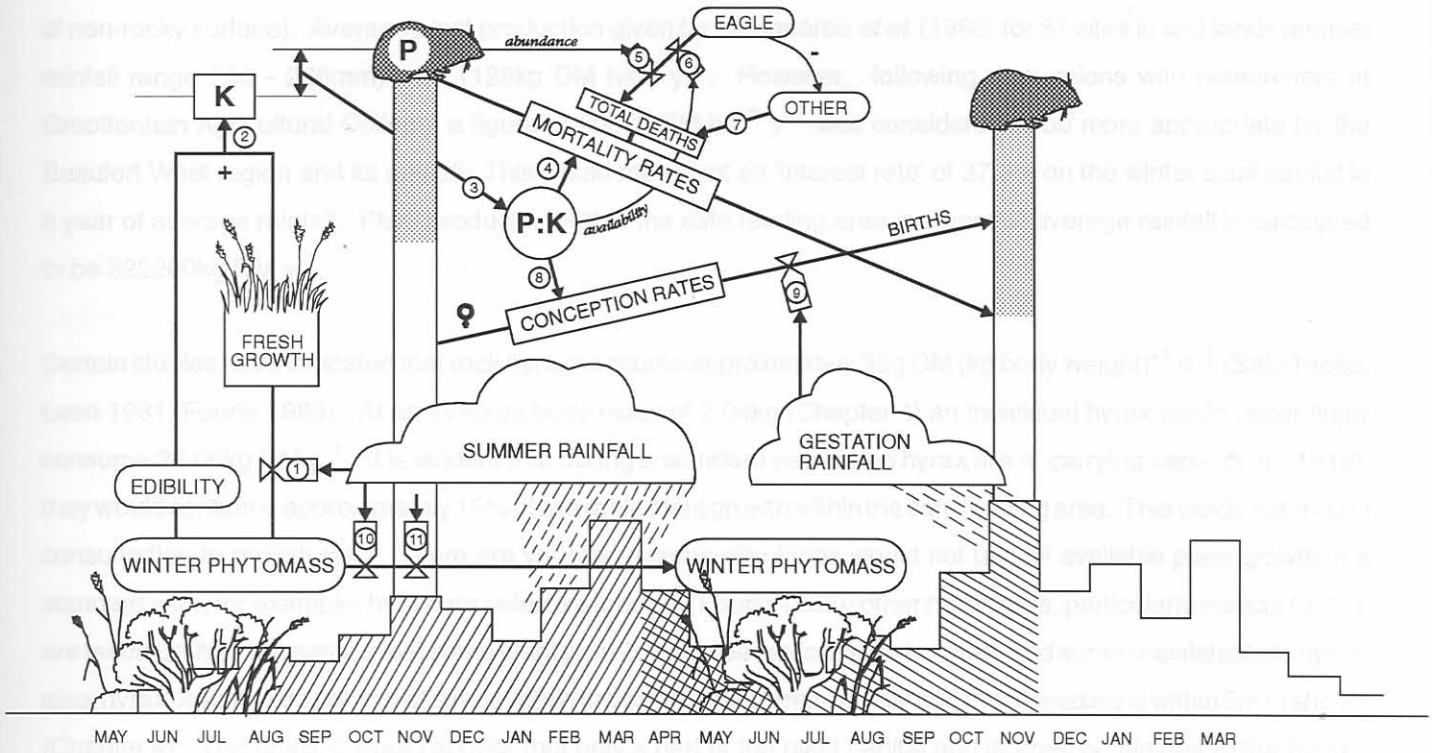



**Figure 110.** Schematic flow-diagram of the hyrax population model. The various steps at each iteration of the model (from one year to the next) are numbered for refering from the text. Shaded histograms at the base of the diagram represent the different rainfall components used by the model. Tall columns represent the hyrax population (P) within a standard eagle territory at each birth-pulse (juvenile component shaded). K is the carrying capacity of food supplies in the vicinity of the refuge habitat. See text for full explanation.

*Lower trophic interaction between vegetation, rainfall and hyrax*

Annual estimates of K derived in this way were very erratic and were an instantaneous reflection of rainfall. They did not take into account the cumulative effects of good or bad years on karoo veld. It was considered that phytomass should improve after good rains and decay slowly during drought; while significant depletion of the phytomass may occur during years of very high consumption by hyrax. Modelling this lower trophic interaction was difficult in the absence of good field data on the response of karoo veld to rainfall and herbivory. The rationale adopted was involved and warrants full explanation. A flow diagram representing the sequence of events in the model may be referred to (Fig. 110). Karoo veld is comprised of grasses and dwarf karoo shrubs, and the latter make up an important winter food for herbivores (Roux *et al.* 1981). For the purposes of this model, fresh growth resulting from the summer rainfall regime could be considered as the 'interest' on the phytomass 'building blocks' or 'capital' remaining at the end of winter.

Estimates of phytomass and plant production for the Karoo are scarce, but Botha (1981 unpubl., in Roux *et al.* 1981) gave a figure of 2415kg dry matter (DM) phytomass $ha^{-1}$ for well managed karoo veld in winter. This would yield an estimate of 864570kg DM for winter plant capital within the safe feeding area in an average eagle territory (358ha

University of Pretoria etd – Davies, R A G (1994)



of non-rocky surface). Average plant production given by Le Houérou *et al.* (1988) for 31 sites in arid lands (annual rainfall range 200 - 266mm) was 1128kg DM $ha^{-1}$ $y^{-1}$. However, following discussions with researchers at Grootfontein Agricultural College, a figure of 900kg DM $ha^{-1}$ $y^{-1}$ was considered to be more appropriate for the Beaufort West region and its rainfall. This would represent an 'interest rate' of 37,3% on the winter plant capital in a year of average rainfall. Plant production within the safe feeding area in a year of average rainfall is calculated to be 322200kg DM $y^{-1}$.

Certain studies have indicated that rock hyrax consume approximately 35g DM (kg body weight)$^{-1}$ $d^{-1}$ (Sale 1966a; Leon 1981; Fourie 1983). At an average body mass of 2,04kg (Chapter 4) an individual hyrax would accordingly consume 26,06kg DM $y^{-1}$. It is evident that during a standard year when hyrax are at carrying capacity (n=1816), they would consume approximately 15% of available plant growth within the safe feeding area. This yields a standard consumption to growth ratio. There are various reasons why hyrax would not use all available plant growth in a standard year, for example: hyrax are selective feeders (Fourie 1983); other herbivores, particularly insects (p. 11), are feeding within the same area; some plant growth would be inaccessible to hyrax; and some unpalatable to hyrax; also, hyrax probably do not use all areas within the safe feeding area equally and much feeding is within 5m of shelter (Chapter 4). Therefore, it would appear that only a part of the plant capital and interest is relevant to the hyrax.

On the assumption that plant capital would be depleted when consumption to growth ratio was greater than the standard ratio, and that capital would accumulate when consumption to growth ratio was lower than the standard ratio, annual change in plant capital was initially modelled on departure from the standard ratio. Allowances had to be incorporated in this sub-routine for the magnitude of the hyrax consumption, as well as the consumption to growth ratio. This 'ratio-dependent' approach has found favour in the emulation of enrichment of lower trophic levels (Slobodkin 1992), but the approach assumes that hyrax consumption and rainfall have an equal and opposing influence on phytomass, and problems arose in the lower trophic model when the removal of predators was artificially simulated. Plants grow in response to rainfall not the absence of herbivory. Removal of plant matter by herbivory is probably far more effective than the decay of phytomass during drought. So it was considered that rainfall would be more involved in the accumulation of phytomass, while consumption by hyrax would be more involved in its depletion.

In order to accommodate this, it became necessary to separate the capital modification into two steps (elements 10 & 11 in Fig. 110). The first step was to modify capital (phytomass) in response to rainfall. A rainfall 'modifier' was derived which would cause capital to accumulate by 25-30% in the very wettest years, and to decay by 5-6% in the very driest years. In any year, the rainfall modifier was selected as a value between 0,94 and 1,30 by linear interpolation based on the difference between rainfall in that year and minimum and maximum long-term rainfall values. Again, a simple linear function had to be assumed here in the absence of detailed field data on the response of karoo veld to rainfall.

The second step represented capital modification in response to herbivory by hyrax. Modelling this interaction proved difficult because the estimates of phytomass consumed by hyrax were minute in comparison to estimates of total phytomass in the safe feeding area. From the estimate that hyrax at standard K (1816) removed only 15%

University of Pretoria etd – Davies, R A G (1994)



of fresh growth in the safe feeding area under conditions of average plant growth, it was assumed that only 15% of the total capital was relevant to the hyrax - the remainder being largely inedible, unpalatable or fed on by other animals. It was decided to reduce winter capital to 15% of its total value and use this in all calculations of the model so that absolute values of growth and consumption could be compared. So in a year of average rainfall the fresh growth on this reduced capital should equal the consumption of 1816 hyrax. In years when consumption was less than fresh growth, it was assumed that hyrax could obtain all their food requirements from the fresh growth, and capital subsequently remained unchanged. In years when consumption was greater than fresh growth, the exact deficit was removed from the (reduced) capital, minus some portion which could be obtained from the less palatable or less accessible phytomass and growth. The latter component was described as the unpalatable buffer, and this was set as 10% of the hyrax food needs that were not met by fresh growth.

Trial runs of the model using this arrangement for capital modification resulted in rates of phytomass change which were in keeping with observations on the decline and recovery periods for karoo biota during major events such as the 1983-84 drought (e.g. see Fig. 59, p. 132), and with the contentions of range managers. Winter capital could totally recover or totally deteriorate between its minimum and maximum limits over about four or five years, in extreme circumstances. For phytomass to show such annual variation in the absence of any stabilising functions in the lower trophic model necessitated upper and lower constraints. Vegetation analyses within and outside the main feeding area of a hyrax colony revealed that edible phytomass was 30% greater beyond the 15m zone (Chapter 4). These analyses were carried out during the dry summer of 1988, and it is estimated that phytomass may have improved by another 30% during wetter conditions. Accordingly, phytomass was generally constrained by 30% above and below the mean value in the model. These constraints are justified on the basis that karoo veld does not change from being a dwarf shrubland even after excellent rains, and that woody, inedible phytomass would always persist even in years of very heavy grazing by hyrax.

In any year, fresh growth on this changing capital was determined in accordance with summer rainfall (e.g. 15% more growth than the usual interest rate, if rainfall was 10% greater than the mean; element 1 in Fig. 110). Total hyrax food resources in a given year were calculated as fresh growth plus the edible component (set at 10% - element 2 in Fig. 110) of the winter capital. Food resources in a standard year can accommodate 1816 hyrax. So the number of hyrax that can be accommodated in a given year was derived by comparing food resources in the given year with standard food resources. This dynamic estimate of K was thus sensitive both to the immediate effects of rainfall, and to the long-term effects of enrichment, or drought and heavy grazing. The annual change in K for a standard run of the model is shown in Figure 111 along with the earlier version of K which was based solely on annual rainfall and fresh growth on a fixed winter capital. The highly erratic behaviour of the latter has been replaced by a more gradual accumulation or depletion of carrying capacity which is considered more realistic for the Karoo. Modelling carrying capacity in this way, it is implicitly assumed that food supply around rocky habitat is limiting, rather than the availability of rock crevices for overnight shelter. In Chapter 4 it was estimated that the mean number of rock crevices per eagle territory (n=4) was 44350 (s.d.=6152). Further rationale to justify this assumption is presented later.

University of Pretoria etd – Davies, R A G (1994)



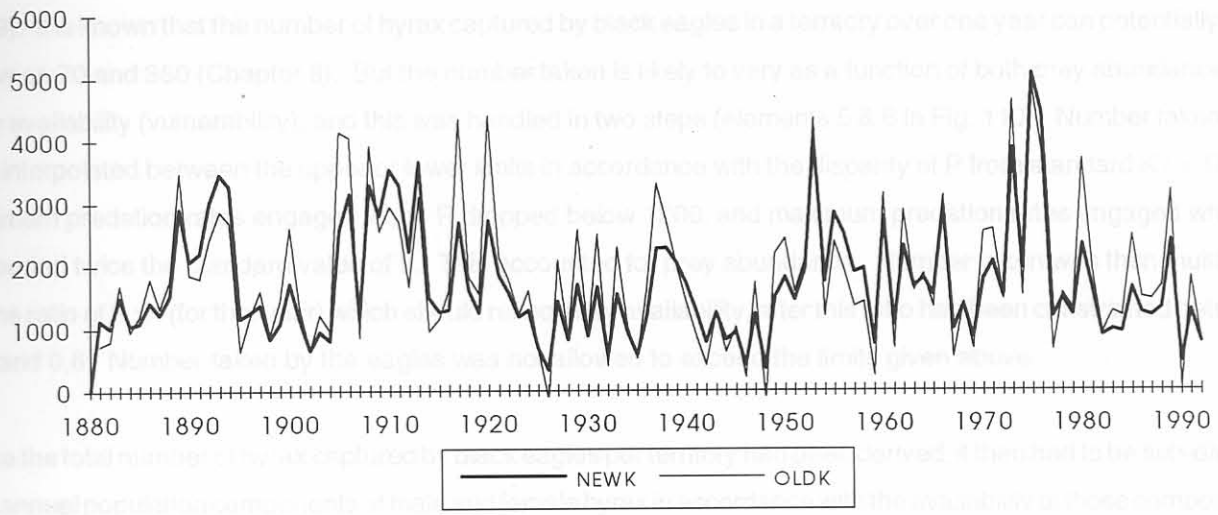



**Figure 111.** Change in two versions of carrying capacity (number of hyrax that can be supported in a standard eagle territory) predicted by a standard run of the model (from 1880 to 1992). One version (OLDK) is based simply on annual rainfall; the other (NEWK) incorporates the influence of cummulative changes in phytomass resulting from good or bad years (see text for full details).

*Pre-natal mortality*

The mortality and fecundity rates for hyrax were interpolated in accordance with the departure of P from K as mentioned earlier (elements 3, 4 & 8 in Fig. 110), but an additional factor was incorporated to represent pre-natal mortality (foetal-resorption) in very dry years (which could not be related to the previous summer rainfall season). Extensive pre-natal mortality was inferred for the very dry period at the end of 1990 (Chapter 4). Pre-natal mortality has also been recorded by Fourie (1983) and Millar (1971). In keeping with the findings of Fourie (1983), correlation analyses in the first part of this chapter revealed that rainfall during the entire gestation period (rather than rain falling late in the gestation period) was most closely related to variation in births, so this component of the rainfall (April - November) was used to modify pre-natal loss (element 9 in Fig. 110). Missing rainfall data for Stolshoek were regressed on Beaufort West data using the following equation: Stolshoek rainfall during gestation = 36,3 + 1,03 * Beaufort West rainfall during gestation ($t=9,2$; $p<0,01$). Foetal resorption was allowed to vary between 2% and 20% (mean = 11%), and this was interpolated on the difference of rainfall during gestation from the long-term mean for this parameter. A similar interpolation was used as an option to explore the potential influence of sex-biased recruitment in response to rainfall (as suggested in Chapters 4 & 10).

University of Pretoria etd – Davies, R A G (1994)



*Removals by black eagles*

Black eagles can be considered specialist predators of rock hyrax and pursue this prey even at low density (Chapters 8 & 9). It is known that the number of hyrax captured by black eagles in a territory over one year can potentially vary between 70 and 350 (Chapter 8). But the number taken is likely to vary as a function of both prey abundance and prey availability (vulnerability), and this was handled in two steps (elements 5 & 6 in Fig. 110). Number taken was first interpolated between the upper or lower limits in accordance with the disparity of P from standard K ( = 1816). Minimum predation rates engaged when P dropped below 1200, and maximum predation rates engaged when P exceeded twice the standard value of K. This accounted for prey abundance. Number taken was then multiplied by the ratio of P : K (for that year) which should reflect prey availability, after this ratio had been constrained between 1,4 and 0,6. Number taken by the eagles was not allowed to exceed the limits given above.

Once the total number of hyrax captured by black eagles per territory had been derived, it then had to be sub-divided into annual population components of male and female hyrax in accordance with the availability of those components in the prey population, and with the preference shown by black eagles for those components. Preference ratings for the various population components were calculated in Chapter 10 (Fig. 93, p. 216), and are given in Appendix 8. Because preference ratings had been derived from field data as percent use of respective components among eagle prey divided by percent availability amongst the prey population, it followed that by multiplying the number of hyrax in each component of the population being modelled by its respective preference rating an artificial population was derived which should reflect the composition of the sample of hyrax that would be taken by the eagles. This artificial population was then proportionally reduced to conform to the number of hyrax that the model predicted the eagles would capture in that particular year. To compare selective with non-selective predation by black eagles, all preference ratings were set to unity.

For standard runs of the model with predators present all mortality could be embraced in one operation, but for the investigation of the influence of age-selective predation, and for the simulated removal of the eagles, it was necessary to separate hyrax captured by black eagles from hyrax dying from other factors (element 7 in Fig. 110). Simply replacing animals that would have died due to eagle predation back into the population to emulate predator-removal did not prove to be a realistic option. As the hyrax population outgrew its carrying capacity in the absence of eagle predation, the model predicted a maximum eagle kill (350 p.a.) - when this inflated 'kill' was returned to the population as survivors at each iteration, the net result was that fewer hyrax were dying from non-eagle mortalities than in a standard run of the model and the simulated removal was grossly exaggerating the influence of the eagles.

To emulate predator removal more realistically, mortality due to eagles and mortality due to other factors had to be modelled separately. Fortunately age-specific mortality to eagles and age-specific mortality to all causes (inclusive mortality) were both known for varying conditions, so age-specific mortality rates due to factors other than eagles could be calculated at each iteration by subtraction during a standard run of the model. Mean, minimum and maximum age-specific mortality rates to factors other than eagles derived in this way are presented in Appendix 9. Test runs of the model (with mortality modelled in two steps) were then conducted to ensure that 'non-eagle' mortality was behaving in the same fashion whether eagles were present or not. In consistent standard runs of the model,

University of Pretoria etd – Davies, R A G (1994)



'non-violent' mortalities (total deaths minus black eagle and caracal kills) were estimated to kill 25,7% of hyrax when total deaths were modelled inclusively, and 25,8% of hyrax when eagle and non-eagle mortalities were modelled separately. The similarity in hyrax population change for standard runs of the model using both inclusive and separated mortality models is shown in Figure 112a. The highly exaggerated effect of eagle removal in the old earlier version is evident in Figure 112b. Separated mortality rates are used for all runs of the model unless otherwise stated.

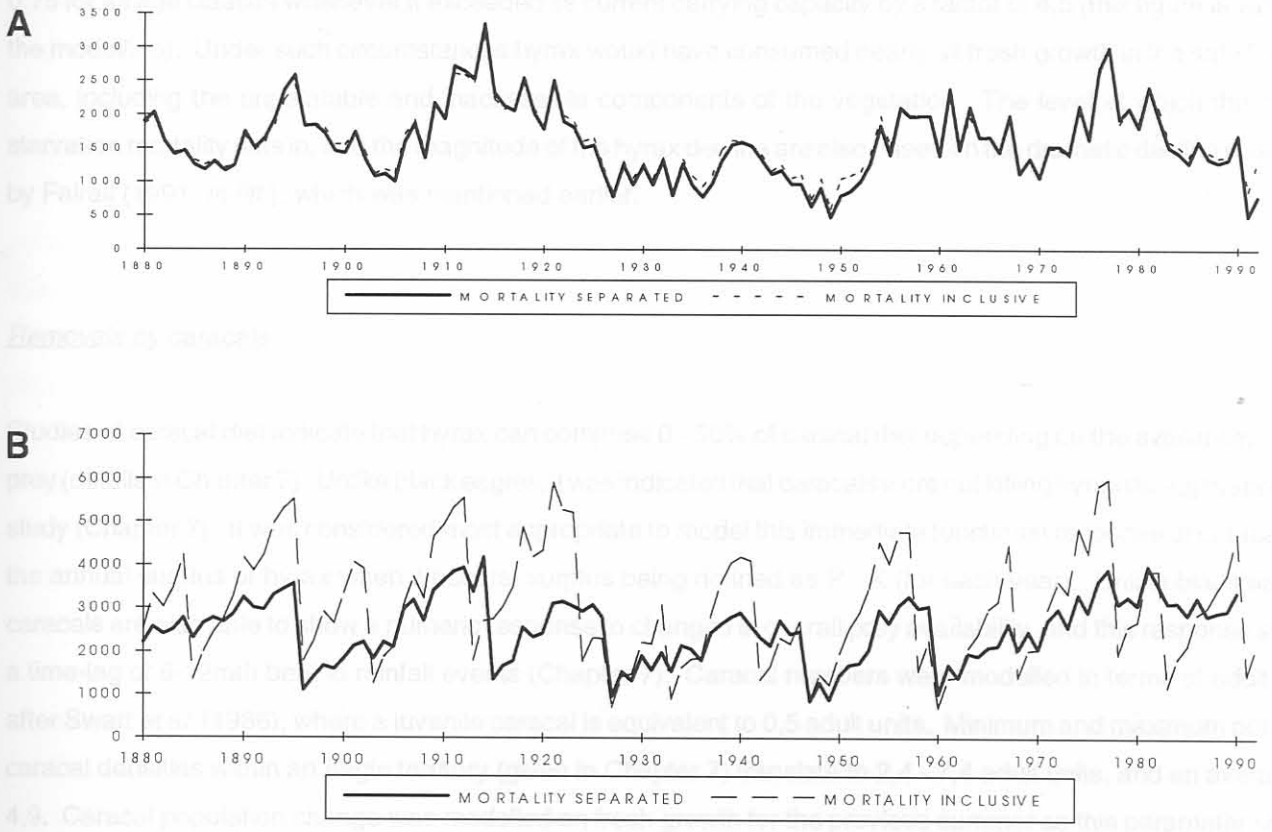



**Figure 112.** Predicted change in hyrax density (per eagle territory) using two model versions with full complement of predation (A) and with eagles removed (B). Mortalities due to eagles were modelled separately from mortalities due to other causes in the updated version. This predicts a very similar pattern of hyrax population change to the old version (inclusive mortality) when predators are present (A) but the old version led to gross exaggeration of the influence of removing eagles (B). See text for a full explanation of why the mortality factors had to be modelled separately.

---

*Compensatory mortality*

It is still not appropriate to assume that all of the potential hyrax prey of black eagles would survive had they not been killed by eagles. A certain component of the potential prey animals would have died anyway. This compensatory mortality was handled in two ways. First, it was assumed that 10% of hyrax captured by black eagles would have died anyway due to old age, accidents and other inevitable causes, irrespective of the prevailing environmental conditions. Old hyrax are highly preferred by the eagles and comprised 16% of all hyrax captured during the study period (Chapter 10). Compensatory mortality due to starvation and disease was treated separately because these

University of Pretoria etd – Davies, R A G (1994)



factors probably only come into play when the hyrax population interacts destructively with vegetation resources. The worst-case figures of inclusive mortality given in Appendix 6 were derived mostly from data gathered during the present study when the hyrax population did not decline dramatically. Therefore these mortality rates would be unlikely to result in a dramatic decline if the hyrax food resources were to collapse. It was important that the same conditions for this starvation and disease mortality should prevail whether predators were removed or not. For the purposes of the model it was assumed that the hyrax population would experience a very heavy mortality rate of 0,75 for all age classes whenever it exceeded its current carrying capacity by a factor of 4,5 (this figure is varied in the modelling). Under such circumstances hyrax would have consumed nearly all fresh growth in the safe feeding area, including the unpalatable and inaccessible components of the vegetation. The level at which this heavy starvation mortality sets in, and the magnitude of the hyrax decline are also based on the dramatic decline observed by Fairall (1991, *in litt.*), which was mentioned earlier.

*Removals by caracals*

Studies of caracal diet indicate that hyrax can comprise 0 - 50% of caracal diet depending on the availability of this prey (details in Chapter 7). Unlike black eagles, it was indicated that caracals were not killing hyrax during the present study (Chapter 7). It was considered most appropriate to model this immediate functional response of caracals on the annual surplus of hyrax when it occurs, surplus being defined as P - K (for each year). Unlike black eagles, caracals are also able to show a numeric response to changes in overall prey availability, and this response shows a time-lag of 6-12mth behind rainfall events (Chapter 7). Caracal numbers were modelled in terms of adult units after Swart *et al.* (1986), where a juvenile caracal is equivalent to 0,5 adult units. Minimum and maximum potential caracal densities within an eagle territory (given in Chapter 7) translate to 2,4 - 7,4 adult units, and an average of 4,9. Caracal population change was modelled on fresh growth for the previous summer as this parameter should provide a good measure of environmental enrichment, and is also used to model hyrax population change (the latter being an important potential prey of caracals). The increase or decline of caracal numbers was not allowed to exceed 30% per annum (Chapter 7) and was derived by a direct linear interpolation on fresh growth, in relation to minimum and maximum values. Numbers were not allowed to exceed the density constraints given above.

Hyrax surplus was divided by the number of caracals to give a measure of availability per predator, after 75% of the number captured by black eagles had been subtracted from the total surplus. Black eagles were given this advantage because they are highly specialised predators of rock hyrax and able to hunt this prey even at low availability - this predation is likely to detract somewhat from the surplus available to the more generalist caracals. It is unlikely that caracals would remove every remaining surplus hyrax but they probably capture a small number of hyrax even when these are well protected (despite the fact that this was not detected by methods employed in the present study). The minimum proportion of hyrax in caracal diet was set at 2% for all years. In years when there was a surplus of hyrax, the proportion of caracal diet made up by this prey was modelled on surplus per caracal. The maximum number of hyrax that may be captured by a single adult caracal is estimated to be 206 p.a. It was assumed that hyrax would comprise a maximum portion of caracal diet (50%) when surplus per caracal exceeded 250.

University of Pretoria etd – Davies, R A G (1994)


The number of hyrax captured per adult caracal was calculated as: the total food requirement of an adult caracal (463 kg p.a. - see Chapter 7) multiplied by the portion of caracal diet in that year that would be comprised of hyrax, and divided by the amount of food available on an average hyrax (1,122kg - see Chapter 8). This value was then multiplied by the number of adult caracal units per eagle territory in that year to yield the total number of hyrax captured by caracals. In the absence of data on age-specific predation by caracals it was assumed that caracals captured the various components of the hyrax population in direct relation to their availability (after Swart *et al* 1986).

*Predator impedance*

Hyrax predation by caracals has not been studied in as much detail as that by black eagles. For most purposes of this model the number of hyrax captured by caracals was estimated but not used in the modelling processes - it was assumed that predation by caracals comprised part of the non-eagle mortality. Predation by caracals could not be separated from remaining mortality factors in the same fashion as black eagle predation because of the poor data, and also because caracal predation was modelled in a very different way (on surpluses). However, it was desirable to know how the model would behave to impedance of both black eagles and caracals in varying degrees of predator persecution. This is termed the predator impedance factor and is considered more appropriate for the karoo situation because caracals are actually more likely to be persecuted than black eagles and neither predators have been totally eradicated. A factor which impedes predators to varying degrees can also be considered on the same continuum as compensatory mortality, which is still a largely unknown element in this system. To run the model on 10% predator impedance, the number of hyrax dying in any given year was computed as: (90% of the potential black eagle kill) + (all non-eagle mortality - 10% of the potential caracal kill). Non-eagle mortality is protected from the effects of inflating eagle kills as described above. Any exaggerations due to inflation of the potential caracal kills impinging on remaining mortality factors could be checked by studying the behaviour of non-predatory mortality with and without impedance. When both predators were impeded by 50%, the portion of hyrax dying non-violently did drop slightly to 24,6%.

*Estimating the cost of hyrax vegetation impact to karoo farmers*

Lensing (1982) calculated that rock hyrax on Namibian farmland in the Karas Mountains do not have a dramatic detrimental effect on farm revenue (less than 1% gross revenue) because livestock do not make extensive use of the rocky habitats favoured by hyrax, and because hyrax use much vegetation which is unavailable to livestock. So any reduction of phytomass by hyrax in the vicinity of rocky habitat is probably not of great financial significance to karoo farmers. Consumption of karoo veld by hyrax can be expected to impinge on the forage resources of domestic livestock when hyrax exceed the immediate carrying capacity of phytomass in the vicinity of rocky habitats and are forced to meet their forage requirements by moving farther from the rocks to feed. The surplus of rock hyrax in such years can effectively be measured as P - K.

University of Pretoria etd – Davies, R A G (1994)



Food consumption by hyrax is given as 35g DM/kg body weight/day (see earlier). Thus an adult hyrax weighing 3,2kg can be expected to consume 112g food per day. This measure will of course depend on the energy content of the feed. Adult Merino sheep on arid rangelands consume about 1,2kg of vegetation (DM) per day (Davies 1985; Short 1985). An adult Merino needs to consume 10,7 times as much food as an adult rock hyrax. Hyrax may need to consume greater quantities of bulk karoo veld than indicated, but they are selective feeders (Fourie 1983) and it is likely that they would choose smaller quantities of energy-rich food from the veld, so the estimate of daily food consumption may not be far wrong.

Kleiber (1975) noted that energy demand was directly related to metabolic weight (body mass$^{0,75}$). Metabolic mass of an adult rock hyrax weighing 3,2kg is calculated as 2,4 kg, and that of an average rock hyrax weighing 2,04kg (Chapter 4) as 1,71kg. Metabolic mass of an adult Merino sheep weighing 45kg (Davies 1985; R. Wilmot pers. comm.; D. Conroy pers. comm.) is calculated as 17,4kg. This indicates that an adult Merino sheep needs to metabolise 7,3 times as much food energy as an adult rock hyrax and 10,2 times as much food energy as an average rock hyrax.

One adult Merino sheep is evidently equivalent to 7,3 - 10,7 rock hyrax in terms of energy and food requirements. For economic calculations at the end of this chapter it is assumed that one adult unit in the domestic sheep population is equivalent to ten units in the hyrax population. A monetary value can be ascribed to grazing requirements given the current (1993) letting rates for karoo veld of approximately R30 per head (small stock) per annum (R. Wilmot pers. comm.; D. Conroy pers. comm.).

University of Pretoria etd – Davies, R A G (1994)



# RESULTS AND DISCUSSION (SECTION 2)

## PREDICTIONS OF THE MODEL -

*Standard run with predators present*

The predicted changes in hyrax numbers, winter phytomass and fresh growth for an average eagle territory near Beaufort West between 1880 and 1992 are shown in Figure 113 for a standard run of the model with predators present. Peaks in hyrax numbers correspond to periods of good growth on undepleted winter phytomass. While declines correspond with drought as expected. Minimum time taken for phytomass to change between upper and lower constraints is about six years, but slightly smaller yet dramatic changes in phytomass take place within a few years, which is considered to be appropriate for karoo veld. Predicted values of P are plotted against the changing estimates of K in Figure 114. Although hyrax numbers do not change as erratically as K, it is clear that under normal circumstances the hyrax population can comfortably track the less sudden but more dramatic changes in carrying capacity brought about through accumulation or depletion of the phytomass. Close tracking of K by P under normal conditions prevents the occurrence of large surpluses of hyrax. Nevertheless, it is estimated that the annual surplus of hyrax in a black eagle territory near Beaufort West averages 466 (with the full complement of predators).

The peaks in hyrax numbers predicted by the model do not correspond to reports in the literature of hyrax irruptions in southern Africa (mainly the Karoo). These irruptions are denoted by asterixes in Figure 113. The reported irruptions all correspond rather to periods of low rainfall and drought following three to seven years after enrichment. It appears from the model that these irruptions were not population explosions at all, but more likely to be major decline phases where large increases in hyrax numbers due to enrichment subsequently experience serious imbalance with food supplies during drought. Under such conditions it is to be expected that food resources in the vicinity of rocky shelter would be depleted and that the hyrax would be forced further from the rocks to feed. At the

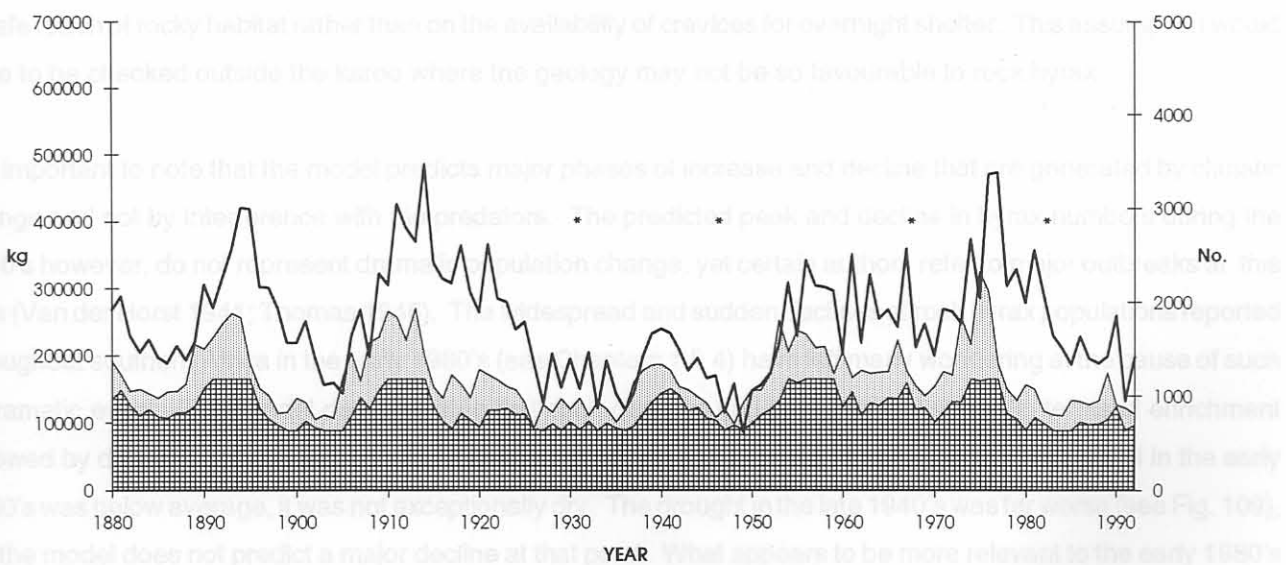



**Figure 113.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data. Asterixes denote timing of hyrax irruptions reported in the literature. Phytomass values are expressed as kg dry matter in the 'safe feeding area'.

University of Pretoria etd – Davies, R A G (1994)



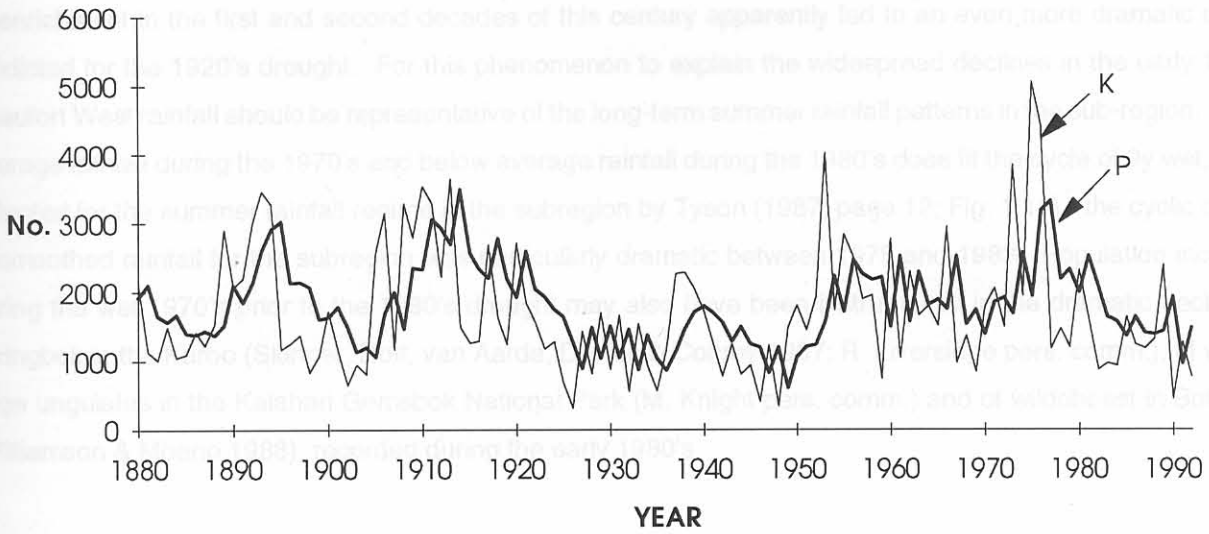



**Figure 114.** Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax (K) and concordant changes in hyrax population density (P) predicted by a standard run of the model with the full complement of predation, using Beaufort West rainfall data.

same time there would be increased pressure to disperse to find more favourable conditions. This would explain colonisation of sub-optimal habitats such as dykes and ditches by hyrax during the said irruptions (Thomas 1946). The irruptions reported in the literature may have been symptomatic of rock hyrax habitat shift and may even have involved mass dispersal more reminiscent of lemming (*Lemmus* spp.) populations (Pitelka 1973; Thompson 1955). The population 'explosions' probably refer to phases when these animals are actually in decline but becoming much more apparent as they are forced from their refuge environment. This hypothesis is in keeping with the observations of increased availability of rock hyrax to black eagles and humans during drought (see methods). Coincidence of reported irruptions with drought suggests that forage in the vicinity of rocks is limiting at high density rather than crevices (for overnight shelter). Rock crevices must have been in sufficient supply to accommodate major population increases during periods of enrichment. Detailed study of rocky habitats (Chapter 3) certainly did not indicate that suitable crevices were in short supply. Therefore it appears justified to model carrying capacity on food supplies in safe reach of rocky habitat rather than on the availability of crevices for overnight shelter. This assumption would have to be checked outside the karoo where the geology may not be so favourable to rock hyrax.

It is important to note that the model predicts major phases of increase and decline that are generated by climatic change and not by interference with the predators. The predicted peak and decline in hyrax numbers during the 1940's however, do not represent dramatic population change, yet certain authors refer to major outbreaks at this time (Van der Horst 1941; Thomas 1946). The widespread and sudden declines of rock hyrax populations reported throughout southern Africa in the early 1980's (see Chapters 1 & 4) have left many wondering at the cause of such a dramatic event. This model demonstrates that such declines can be explained simply in terms of enrichment followed by drought, with no additional involvement of disease or predator eradication. While rainfall in the early 1980's was below average, it was not exceptionally dry. The drought in the late 1940's was far worse (see Fig. 109), yet the model does not predict a major decline at that point. What appears to be more relevant to the early 1980's decline is the pronounced build up in hyrax numbers during the wet 1970's which can mostly be attributed to two major birth pulses in the very wet summers at the end of 1976 and 1977. Major increases in hyrax numbers due

University of Pretoria etd – Davies, R A G (1994)



to enrichment in the first and second decades of this century apparently led to an even more dramatic decline predicted for the 1920's drought. For this phenomenon to explain the widespread declines in the early 1980's, Beaufort West rainfall should be representative of the long-term summer rainfall patterns in the sub-region. Above average rainfall during the 1970's and below average rainfall during the 1980's does fit the cycle of 9y wet, 9y dry detected for the summer rainfall regime in the subregion by Tyson (1987; page 12; Fig. 1.11) - the cyclic change in smoothed rainfall for the subregion was particularly dramatic between 1975 and 1983. Population increases during the wet 1970's prior to the 1980's drought may also have been instrumental in the dramatic declines of springbok in the Karoo (Skinner, Dott, van Aarde, Davies & Conroy 1987; R. Liversidge pers. comm.), of various large ungulates in the Kalahari Gemsbok National Park (M. Knight pers. comm.) and of wildebeest in Botswana (Williamson & Mbano 1988), recorded during the early 1980's.

*Linking conception rates to rainfall patterns*

A different pattern emerges for a standard run of the model if conception rates are interpolated (linearly) on summer rainfall rather than P:K ratio (Fig. 115). As expected, the hyrax population is less influenced by the immediate erratic behaviour of K, but still follows gradual accumulation or depletion of phytomass in a smoother, more fluid fashion. There appears to be more of a 'wave action' in hyrax numbers when conception is modelled on rainfall only, with two major peaks separated by about 60y. Increase in the major peaks can be attributed to large birth pulses at high population density when conception is only affected by rainfall. Disparity between the two versions is somewhat reduced if phytomass constraints are tighter when conception is modelled on rainfall only, leading to a reduction in major peaks and an increase in minor peaks. Modelling conception on rainfall only may be appropriate for the study period when population density was relatively low, but the absence of a crowding effect on reproduction (well demonstrated in other animals) is considered unrealistic. Elements from both versions are probably involved in the real situation, but for this study conception is modelled on P:K ratio for all standard runs of the model unless otherwise stated.

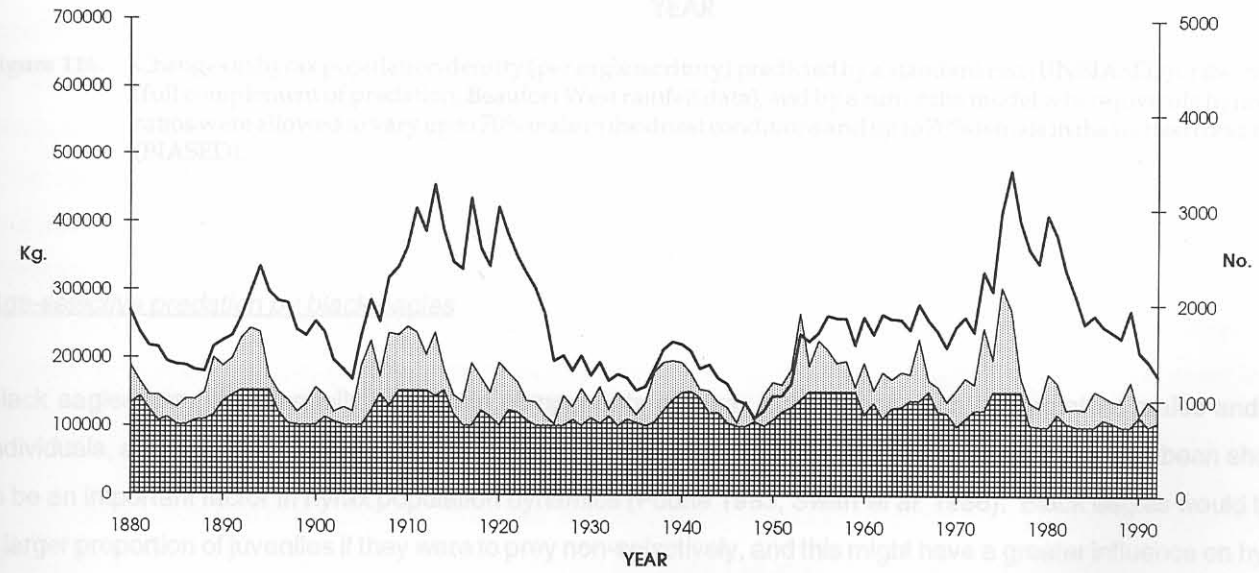



**Figure 115.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a standard run of the model with the full complement of predation (using Beaufort West rainfall data), but in this case with hyrax conception rates modelled on preceding summer rainfall rather than P:K ratio.

University of Pretoria etd – Davies, R A G (1994)



*The potential influence of a bias in recruitment of the sexes*

The influence of certain demographic processes on hyrax numbers can be investigated with standard runs of the model with predators present. In Chapters 4 & 10 it was indicated from three lines of field evidence that more male hyrax are recruited in dry years and more females in wet years. It is conceivable that such bias might have a destabilising influence on hyrax population density because greater production of males and impaired production of females in dry conditions should impair the ability of the population to grow, whereas the converse would hold for wet conditions. However this was not indicated when juvenile sex ratios in the model were allowed to vary up to 70% male in the years of least rainfall during the gestation period, and up to 70% female in the years of most rainfall during the gestation period. This run of the model is compared with a standard run in Figure 116. There was no significant difference in the variation of population density ($F=1,07$; $p=0,37$), in the mean population size ($z=0,30$; $p=0,38$), or in the distribution of values of population density (Smirnov test: $T=0,08$; $p>0,20$) for these two runs of the model. It is concluded that any rainfall-related bias in recruitment of the sexes would not have a significant effect on rock hyrax population change.

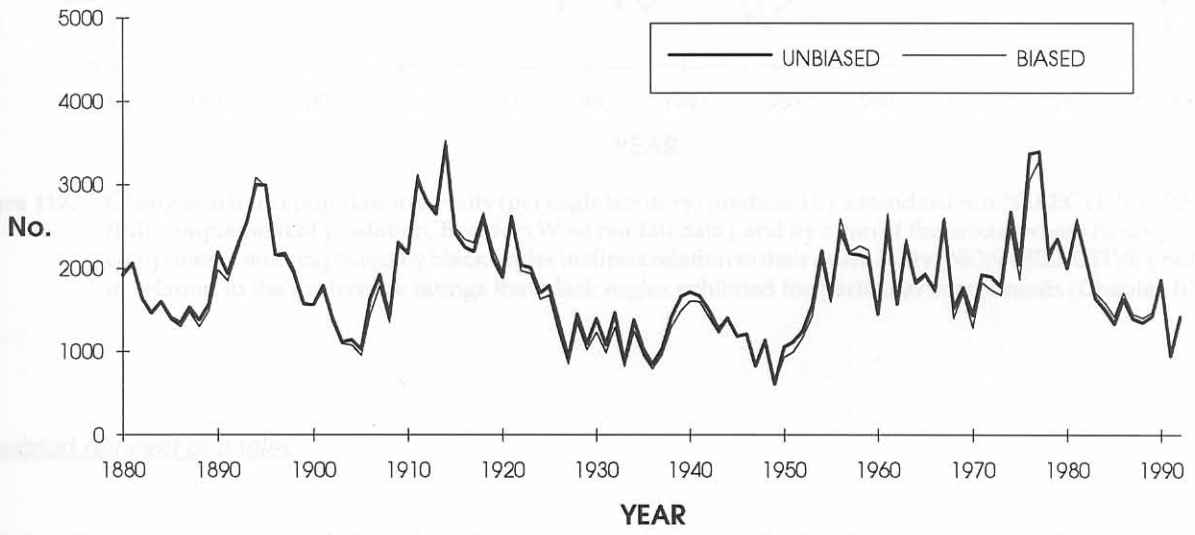



**Figure 116.** Changes in hyrax population density (per eagle territory) predicted by a standard run (UNBIASED) of the model (full complement of predation, Beaufort West rainfall data), and by a run of the model where juvenile hyrax sex ratios were allowed to vary up to 70% male in the driest conditions and up to 70% female in the wettest conditions (BIASED).

*Age-selective predation by black eagles*

Black eagles prey preferentially on certain components of hyrax populations such as immature males and old individuals, and show low preference or avoidance for juveniles (Chapter 10). Juvenile mortality has been shown to be an important factor in hyrax population dynamics (Fourie 1983; Swart *et al.* 1986). Black eagles would take a larger proportion of juveniles if they were to prey non-selectively, and this might have a greater influence on hyrax population change. To test for any differences in hyrax demography due to age-selective or non-selective predation by black eagles, eagles were assumed to take hyrax individuals in direct proportion to their availability in one run

University of Pretoria etd – Davies, R A G (1994)



of the model and this was compared with a standard run where hyrax were captured in relation to both availability and preference rating (Figure 117). No significant differences were detected in the variation of population density ($F=1,04$; $p=0,44$), in the mean population size ($z=0,27$; $p=0,39$), or in the distribution of values of population density (Smirnov test: $T=0,07$; $p>0,20$) between the results. The pattern of age-specific predation by black eagles on rock hyrax is evidently not of great significance to hyrax population change. However, it should be noted that due to the dynamic nature of the model, any short-term effects of such factors may be compensated for in the long-term by changes in mortality or recruitment.

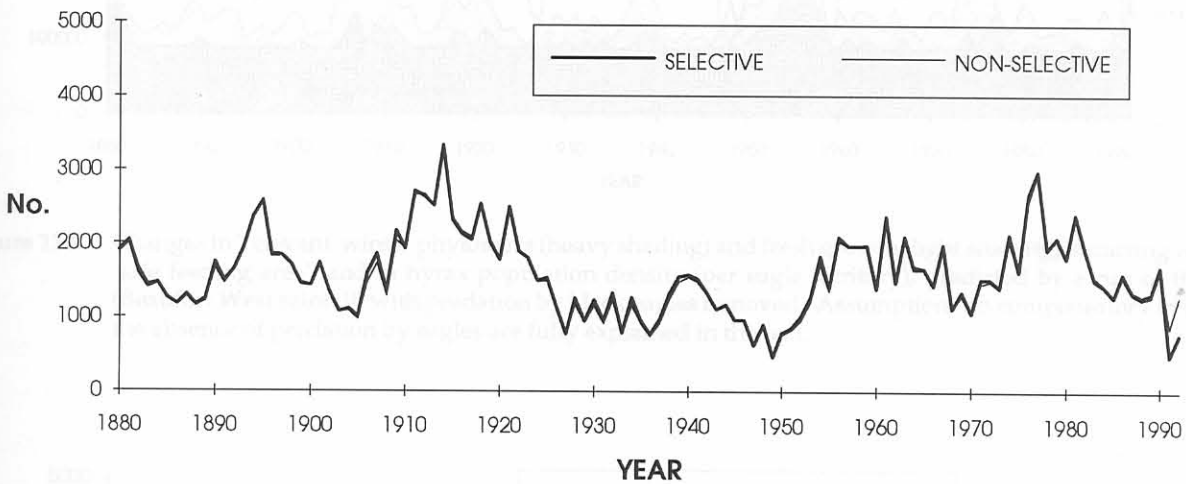



**Figure 117.** Changes in hyrax population density (per eagle territory) predicted by a standard run (SELECTIVE) of the model (full complement of predation, Beaufort West rainfall data), and by a run of the model where hyrax population components were captured by black eagles in direct relation to their availability (NON-SELECTIVE), rather than in relation to the preference ratings that black eagles exhibited for particular components (Chapter 10).

*Simulated removal of eagles*

In contrast to the above, removal of black eagles has a very dramatic effect on hyrax population change as predicted by the model (Figs. 118 & 119). In this removal simulation it was assumed that 10% of the potential black eagle kill would have died anyway from inevitable factors (as justified in the methods section). A far more rapid rate of growth of the hyrax population is predicted in the absence of eagles and consequently the population density regularly rises to a level where it is estimated that food resources can no longer support the population and major compensatory mortality due to starvation and disease set in. The population reaches this critical limit ($4,5*K$) seven times in the last century for runs of the model when eagles are removed, and not once for runs of the model when eagles are present. One such crash in the absence of eagles coincides with the 1983 drought following enrichment in the 1970's.

The model predicts that in the absence of eagles hyrax numbers are sufficient to depress phytomass in the vicinity of their refuge habitat by about 17%. This is apparent in Figure 118, and only in very wet periods is the phytomass able to increase from its lower constraint. Accordingly, carrying capacity set by edible phytomass and fresh growth on total phytomass is also reduced by a similar proportion. Despite this, mean hyrax numbers are predicted to be

University of Pretoria etd – Davies, R A G (1994)



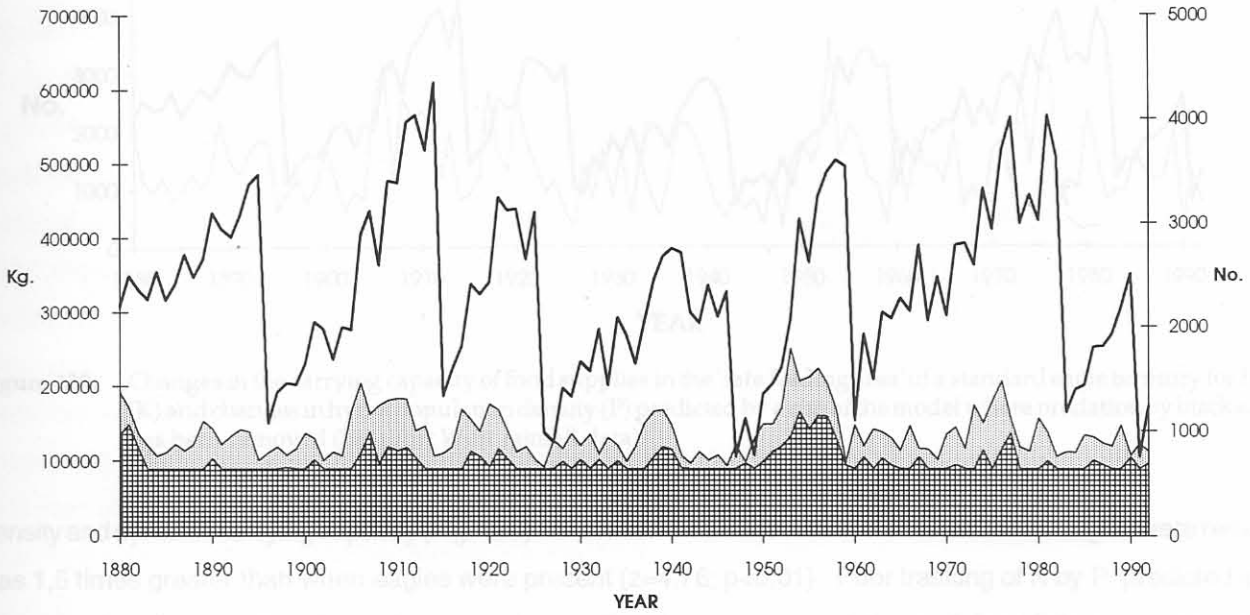



**Figure 118.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model (Beaufort West rainfall) with predation by black eagles removed. Assumptions on compensatory mortality in the absence of predation by eagles are fully explained in the text.

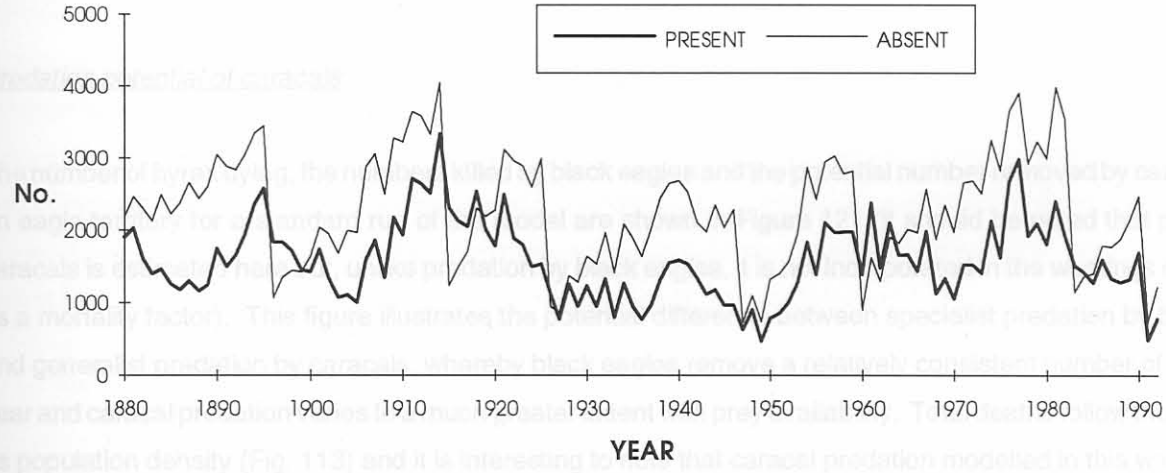



**Figure 119.** Hyrax population change predicted by the model (Beaufort West rainfall) with predation by black eagles PRESENT and ABSENT.

32% higher in runs of the model when eagles are removed. In comparison with a standard run of the model (eagles present; see Fig 119), this difference is statistically highly significant ($z=5,90$; $p<0,01$). The same comparison also revealed highly significant statistical differences in the variability of population density ($F=2,08$; $p<0,01$) and in the distribution of population density values (Smirnov test: $T=0,34$; $p<0,01$). Variability in population density when eagles were removed, as measured by the coefficient of variation (s.d./mean), was 6% larger than variability with eagles present. Much of this can of course be attributed to the predicted crashes. It would appear that diminished removals from the hyrax population in the absence of black eagles prevents close tracking between population

University of Pretoria etd – Davies, R A G (1994)



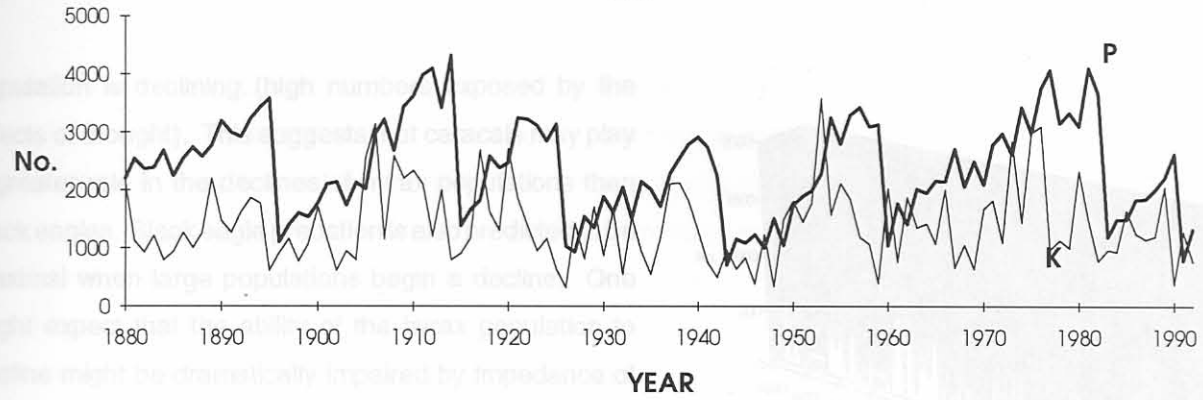



**Figure 120.** Changes in the carrying capacity of food supplies in the 'safe feeding area' of a standard eagle territory for hyrax (K) and changes in hyrax population density (P) predicted by a run of the model where predation by black eagles has been removed (Beaufort West rainfall data).

density and dynamic carrying capacity (Fig. 120). The mean annual deviation of P from K when eagles were removed was 1,5 times greater than when eagles were present ($z=4,76$; $p<0,01$). Poor tracking of K by P, predicted in the absence of eagles, results in larger hyrax surpluses. If eagles are removed, the model predicts an average annual surplus of 1088 hyrax. Accurate prediction of hyrax surpluses depends mostly on correct estimation of standard carrying capacity and correct handling of compensatory mortality in the absence of eagles. These matters are treated further under sensitivity analysis. In theory then, removal of black eagles should have a dramatic effect upon hyrax population change. Certain predator removal experiments have provided empirical evidence demonstrating such a dramatic effect upon other prey populations (see p. 256).

*Predation potential of caracals*

The number of hyrax dying, the numbers killed by black eagles and the potential number removed by caracals within an eagle territory for a standard run of the model are shown in Figure 121 (it should be noted that predation by caracals is estimated here but, unlike predation by black eagles, it is not incorporated in the workings of the model as a mortality factor). This figure illustrates the potential difference between specialist predation by black eagles and generalist predation by caracals, whereby black eagles remove a relatively consistent number of hyrax every year and caracal predation varies to a much greater extent with prey availability. Total deaths follow the same trend as population density (Fig. 113) and it is interesting to note that caracal predation modelled in this way is minimal while the population increases (population well protected during periods of enrichment), and maximal while the

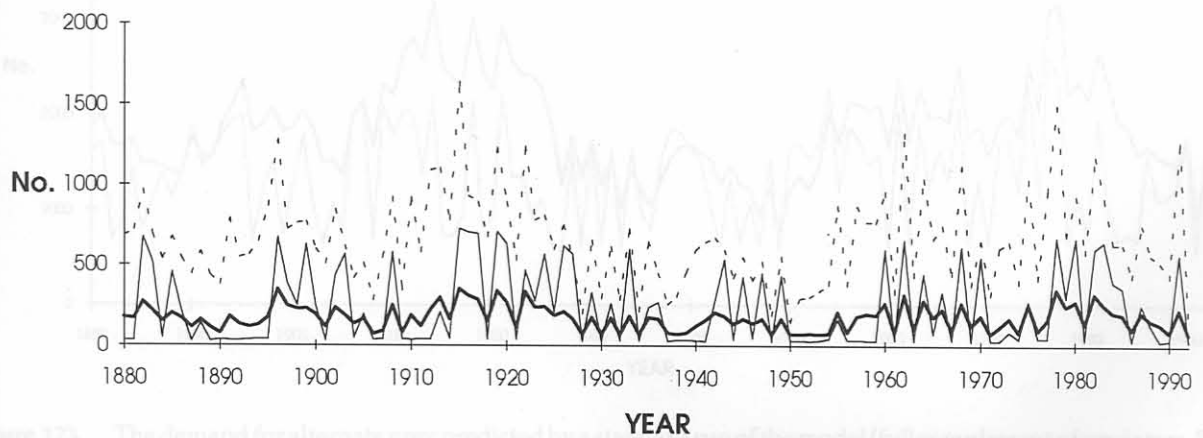



**Figure 121.** Total number of hyrax dying (broken line), hyrax kill by eagles (heavy line) and potential hyrax kill by caracals (faint line) as predicted by a standard run of the model (full complement of predation, Beaufort West rainfall).

University of Pretoria etd – Davies, R A G (1994)



population is declining (high numbers exposed by the effects of drought). This suggests that caracals may play a greater role in the declines of hyrax populations than black eagles. Black eagle predation is also predicted to be maximal when large populations begin a decline. One might expect that the ability of the hyrax population to decline might be dramatically impaired by impedance of these predators. On account of their greater consumption rates, numeric and functional responses, caracals have a much greater potential for removing hyrax surpluses (Fig. 122) than black eagles. Although caracals did not reach their maximum potential population density in a standard run of the model, the range in the number of hyrax that they removed was three times that of black eagles. Had caracals realised their full predation potential, this difference would have been nearly five-fold.

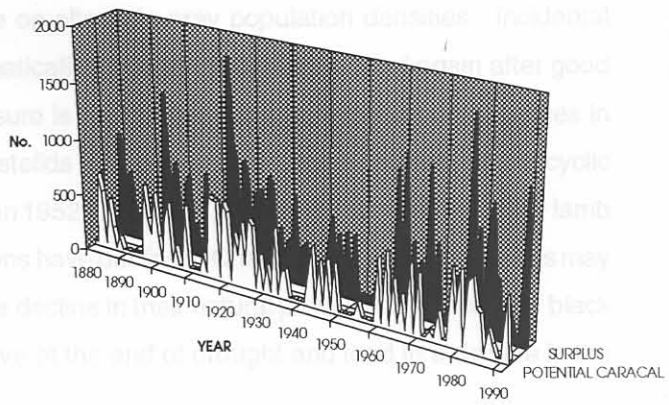



**Figure 122.** Annual surplus (P-K) of hyrax (dark shaddow), and potential hyrax kill by caracals (white peaks) as predicted by a standard run of the model (full complement of predation, Beaufort West rainfall data).

*The demand for alternate prey*

By calculating the total number of prey captured by both predator species, and then removing from this the number of hyrax captured, it is possible to predict the demand for alternate prey. This is plotted against hyrax numbers in Figure 123 for a standard run of the model. In keeping with the prediction that predation of rock hyrax by black eagles and caracals is maximal during decline phases, the demand for alternate prey is evidently maximal during the increase phase of the hyrax population when hyrax are less available. On a shorter time-scale, demand for alternate prey is high in wet years and low in dry years. Time-lapse photography indicated that non-hyrax prey of black eagles

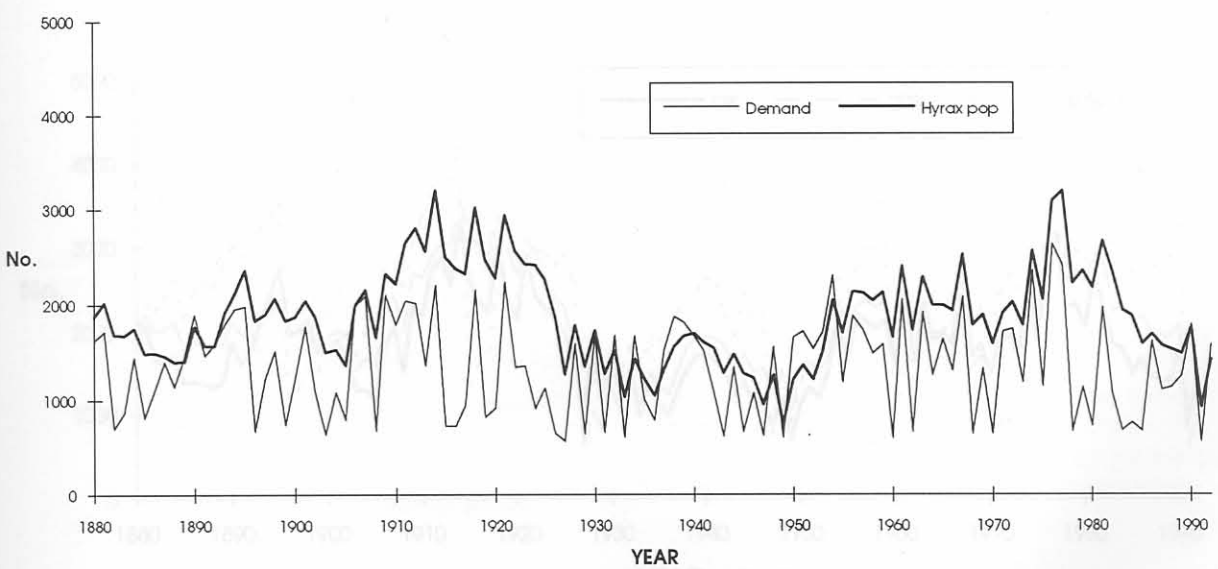



**Figure 123.** The demand for alternate prey predicted by a standard run of the model (full complement of predators, Beaufort West rainfall data) as total prey captured by black eagles and caracals minus hyrax prey captured by black eagles and caracals. Predicted changes in hyrax population density is shown for reference (heavy line).

University of Pretoria etd – Davies, R A G (1994)



featured least in eagle diet in the dry year of 1988, and most in 1989 when good rains arrived (Chapter 9: Fig. 83, p. 198). This variable predation may have had an influence on alternate prey population densities. Incidental observations of red rock rabbits in the KRNP increased dramatically through 1988 and declined again after good rains at the end of 1989 (Chapter 5). Heavy predation pressure is held responsible for synchronous declines in alternate prey species such as game birds and even mustelids (Korpimäki & Norrdahl 1989c) when cyclic populations of small mammals or snowshoe hares crash (Hagen 1952; Lack 1954). Farmers complain of heavy lamb losses to predators during drought when natural prey populations have declined (Chapter 11). For caracals this may be so, especially when high densities of caracals experience a decline in their natural prey, but in the case of black eagles stock predation is most likely to occur when rains arrive at the end of drought and lead to a decline in the availability of already reduced hyrax populations.

*Impeding both predators*

Total removal of black eagles is an unrealistic scenario for the Karoo where caracals are more likely to be persecuted by farmers, and where persecution seldom leads to total eradication of either. Impedance of both predators (see methods) is much more realistic and can be modified to investigate the influence of different levels of persecution. This type of analysis is also less demanding with respect to the largely unknown element of compensatory mortality and permits incorporation of the effect of caracals into the workings of the model for the first time.

Changes in hyrax population density for 0% 20% and 40% impedance of both predators are shown in Figure 124. A similar pattern of hyrax population change to that for removal of the eagles (Fig. 118) is achieved by a 40% impedance of both predators. Diminished removals from the hyrax population with progressive impedance of predators is manifest as a more rapid rate of increase during enrichment and impaired decline during drought. At higher levels of impedance, sporadic crashes caused by great discrepancy between P and K can even lead to population increases at times when otherwise the population would be declining. The predicted increase in hyrax

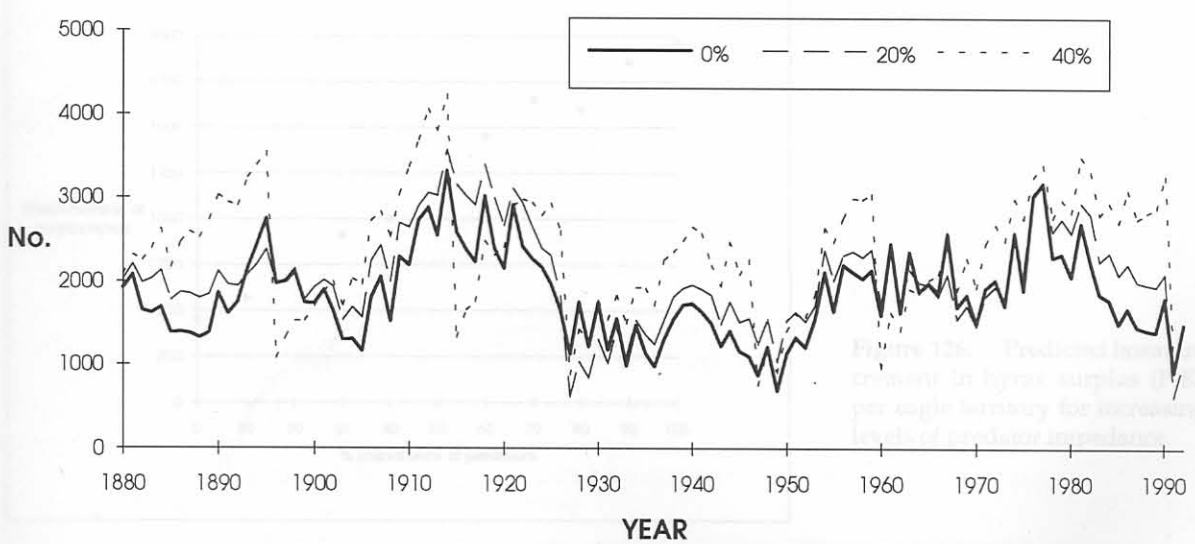



**Figure 124.** Predicted changes in hyrax population density for different runs of the model (Beaufort West rainfall data) with varying levels of predator 'impedance' - see text for method.

University of Pretoria etd – Davies, R A G (1994)



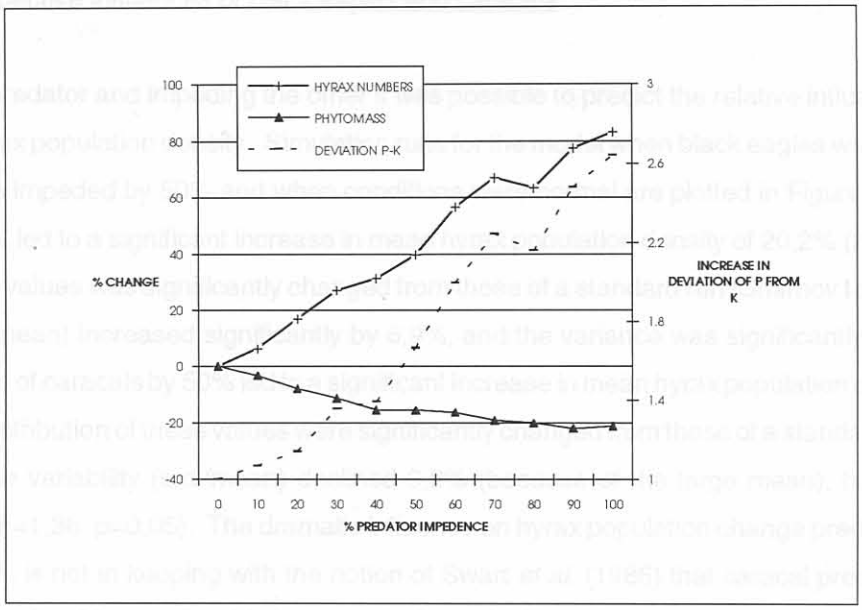



**Figure 125.** Predicted increment of average hyrax population density and population variability (as measured by the difference of P from K), and decrement of average winter phytomass, for increasing levels of predator impedance.

population density, deviation of P from K, and the reduction in phytomass for increasing levels of predator impedance are plotted in Figure 125. Here deviation of P from K illustrates changes in the variability of population density. Variance in population density becomes significantly different from that in a standard run of the model when predators are impeded by 30% (F=1,73; p<0,01). The mean hyrax population density and the distribution of these values become significantly different from those for a standard run of the model when predators are impeded by only 10% (z=-3,77; p<0,01; Smirnov test: T=0,30; p<0,01). Phytomass is not much reduced beyond 40% impedance on account of lower constraints on this parameter. The relative increase of mean hyrax population density is a linear function with predator impedance leading to a linear increase in hyrax surpluses (Fig. 126).

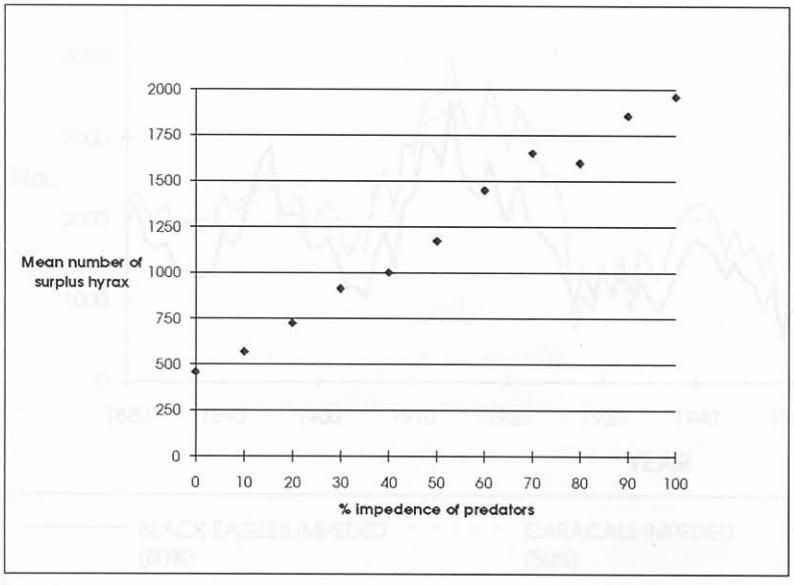



**Figure 126.** Predicted linear increment in hyrax surplus (P-K) per eagle territory for increasing levels of predator impedance.

University of Pretoria etd – Davies, R A G (1994)



*Contrasting the respective influences of black eagles and caracals*

By controlling one predator and impeding the other it was possible to predict the relative influence of black eagles and caracals on hyrax population density. Simulation runs for the model when black eagles were impeded by 50%, when caracals were impeded by 50% and when conditions were normal are plotted in Figure 127. Impedance of black eagles by 50% led to a significant increase in mean hyrax population density of 20,2% ($z=-4,13$; $p<0,01$); the distribution of these values was significantly changed from those of a standard run (Smirnov test: $T=0,30$; $p<0,01$); the variability (s.d./mean) increased significantly by 6,9%, and the variance was significantly increased ($F=1,65$; $p<0,01$). Impedance of caracals by 50% led to a significant increase in mean hyrax population density of 21,1% ($z=-4,58$; $p<0,01$); the distribution of these values were significantly changed from those of a standard run (Smirnov test: $T=0,35$; $p<0,01$); the variability (s.d./mean) declined 3,8% (because of the large mean), but variance was still significantly larger ($F=1,36$; $p=0,05$). The dramatic influence on hyrax population change predicted when caracals are impeded by 50% is not in keeping with the notion of Swart *et al.* (1986) that caracal predation merely tracks changes in hyrax density. More noticeable increase in the variability of hyrax population density under black eagle impedance rather than caracal impedance could be attributed to the additional hyrax population crash predicted in 1960.

There was some suggestion then that impedance of black eagles had more influence on hyrax population change than impedance of caracals, especially at peak prey densities (Fig. 127). This was contrary to expectations based on the greater potential of caracals to remove hyrax surpluses, and indicates the importance of a demographic factor which consistently removes a number of the hyrax population. Significant differences in mean population density, in the distribution of density values, and in the variances of population density between black eagle impedance and caracal impedance could not be demonstrated statistically. However predation by black eagles was free to compensate for changes in prey density when caracals were impeded whereas the reverse situation was not true and this may have influenced the result. Also, caracal predation of hyrax is not yet based on accurate data.

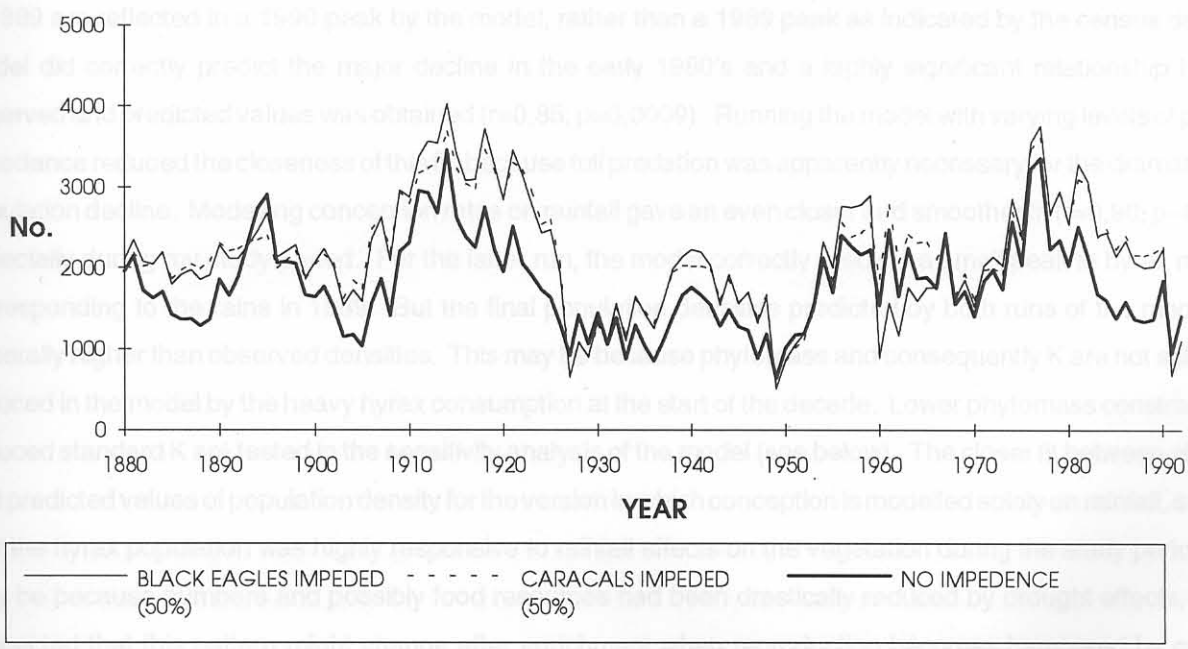



**Figure 127.** The predicted departure of hyrax population change from a standard run of the model (NO IMPEDANCE, Beaufort West rainfall) when black eagles are impeded by 50% and when caracals are impeded by 50%.

University of Pretoria etd – Davies, R A G (1994)



ASSESSMENT OF THE MODEL -

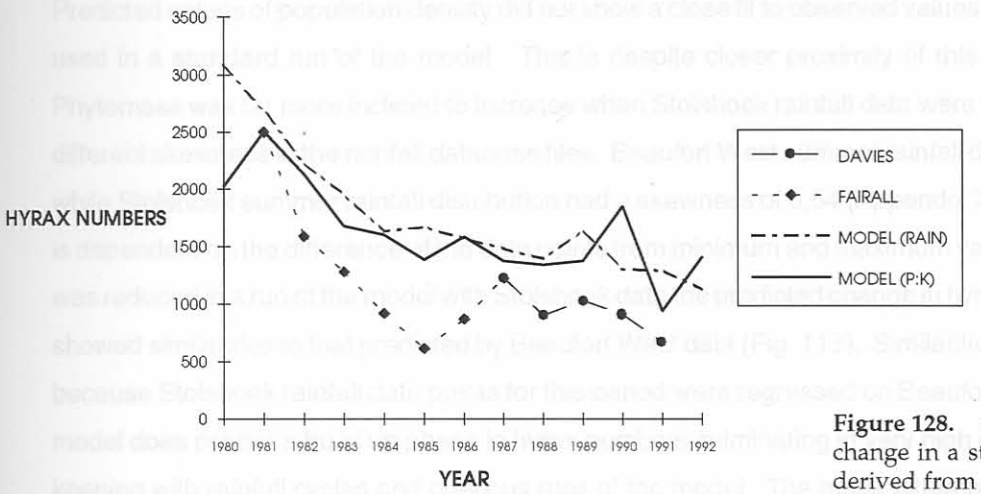



**Figure 128.** Observations of hyrax population change in a standard eagle territory in the KRNP derived from counts at colonies by Fairall (in litt.) and Davies (the present study), in comparison with predictions of hyrax population change after a full standard run of the model with hyrax conception based both on rainfall and on P:K ratio.

*Fit to hyrax census data*

In Figure 128 estimates of hyrax population density per average eagle territory in the KRNP are plotted against predicted values for population density from 1980 through until 1992. Estimates of population density (per eagle territory) were extrapolated from data on group size gathered from counts at 16 colonies conducted during the present study (1987 - 1991), and from counts at two of these colonies conducted by Fairall (*in litt.*) for the preceding period from 1981 until 1987. Predicted values are derived from running the model on the entire rainfall database (1880 - 1992) with conception rates modelled on P:K ratio (standard run) and on rainfall. Although predicted values derived from a standard run did not closely match estimates of population density during my study period (good rains in 1989 are reflected in a 1990 peak by the model, rather than a 1989 peak as indicated by the census data), the model did correctly predict the major decline in the early 1980's and a highly significant relationship between observed and predicted values was obtained (r=0,85; p=0,0009). Running the model with varying levels of predator impedance reduced the closeness of this fit, because full predation was apparently necessary for the dramatic hyrax population decline. Modelling conception rates on rainfall gave an even closer and smoother fit (r=0,90; p=0,0002), especially during my study period. For the latter run, the model correctly predicts a small peak in hyrax numbers corresponding to the rains in 1989. But the final population densities predicted by both runs of the model were generally higher than observed densities. This may be because phytomass and consequently K are not sufficiently reduced in the model by the heavy hyrax consumption at the start of the decade. Lower phytomass constraints and reduced standard K are tested in the sensitivity analysis of the model (see below). The closer fit between observed and predicted values of population density for the version in which conception is modelled solely on rainfall, suggests that the hyrax population was highly responsive to rainfall effects on the vegetation during the study period. This may be because numbers and possibly food resources had been drastically reduced by drought effects, but it is suspected that this pattern might change after enrichment when reproduction becomes hampered by crowding effects at high population density.

University of Pretoria etd – Davies, R A G (1994)



*Different rainfall regimes*

Predicted values of population density did not show a close fit to observed values when Stolshoek rainfall data were used in a standard run of the model. This is despite closer proximity of this collection site to the study area. Phytomass was far more inclined to increase when Stolshoek rainfall data were used. This may have been due to different skewness in the rainfall database files. Beaufort West summer rainfall distribution had a skewness of 0,84 while Stolshoek summer rainfall distribution had a skewness of 0,54 (Appendix 7). Phytomass response to rainfall is dependent on the difference of the data points from minimum and maximum values. When phytomass sensitivity was reduced in a run of the model with Stolshoek data the predicted change in hyrax population density (Figure 129) showed similarities to that predicted by Beaufort West data (Fig. 113). Similarities prior to 1929 are to be expected because Stolshoek rainfall data points for this period were regressed on Beaufort West rainfall. But this run of the model does predict a build up phase in hyrax numbers culminating in very high population density in the 1970's in keeping with rainfall cycles and previous runs of the model. The major difference when Stolshoek data are used is that the model does not predict a major decline in hyrax numbers in the early 1980's. This can be attributed to the unexpected finding that Stolshoek rainfall in the early 1980's was not markedly below average. All summer rainfall for this period was average or above average except for summer rainfall at the end of 1982 which was 30% lower than normal. It is not clear why Stolshoek data did not indicate drought in the early 1980's which was reported to be widespread (Tyson 1983, 1986). Perhaps the location of this collection site in the foothills of the Nuweveldberg mountains experienced more consistent amounts of orographic rain.

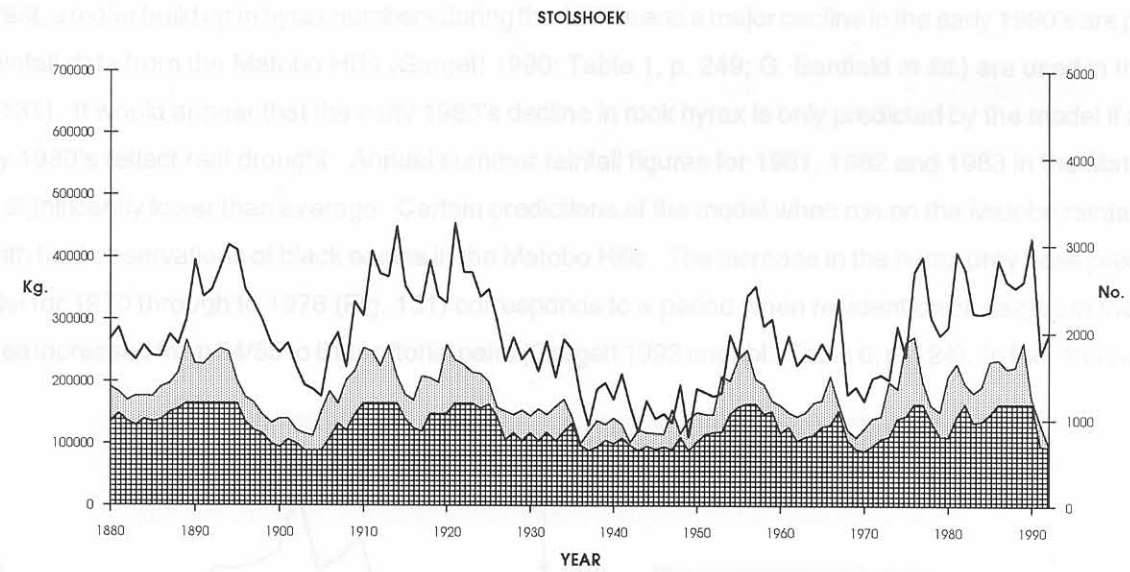



**Figure 129.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using rainfall data recorded for Stolshoek.

It was more surprising to discover that rainfall for the Beaufort West district (32 sites) was also average to above average for the same period except for summer rain at the end of 1982 (30% lower than normal). This might also be due to the proximity of the continental escarpment. In keeping with predictions using Beaufort West rainfall, a run of the model using district rainfall data (Figure 130) revealed hyrax declines corresponding to droughts in the

University of Pretoria etd – Davies, R A G (1994)



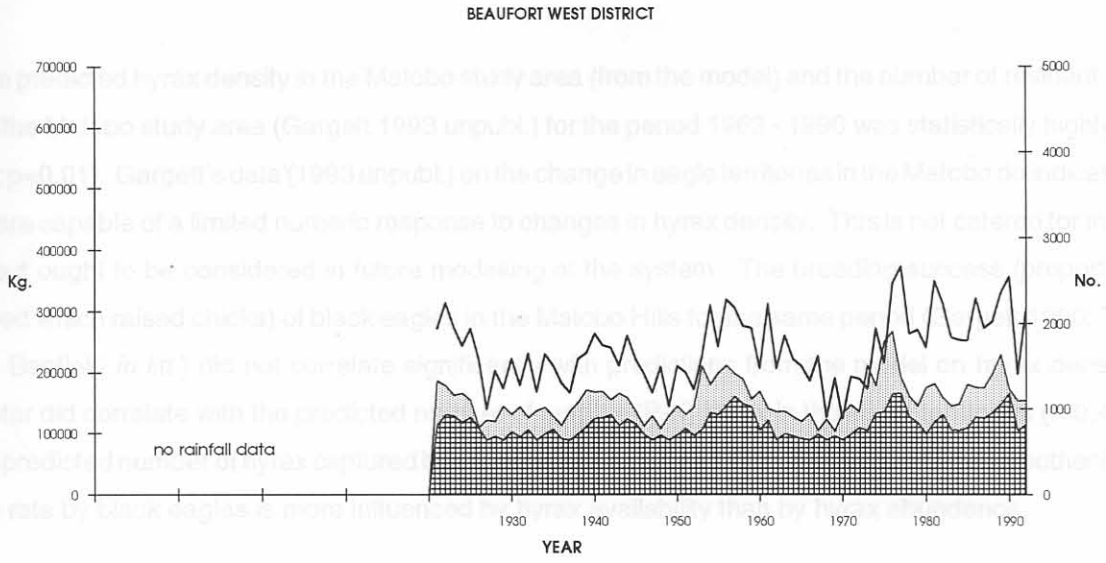



**Figure 130.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using the average of rainfall data recorded for 32 stations in the Beaufort West District.

early 1930's and the late 1940's, and a build up phase which began in the 1950's and culminated in very high densities in the 1970's. But again no major decline is predicted for the early 1980's and this can also be attributed to the apparent absence of drought in the rainfall database for that period.

By contrast, a major build up in hyrax numbers during the 1970's and a major decline in the early 1980's are predicted when rainfall data from the Matobo Hills (Gargett 1990: Table 1, p. 249; G. Banfield *in litt.*) are used in the model (Figure 131). It would appear that the early 1980's decline in rock hyrax is only predicted by the model if rainfall in the early 1980's reflect real drought. Annual summer rainfall figures for 1981, 1982 and 1983 in the Matobo Hills were all significantly lower than average. Certain predictions of the model when run on the Matobo rainfall pattern tallied with field observations of black eagles in the Matobo Hills. The increase in the hyrax prey base predicted by the model for 1970 through to 1978 (Fig. 131) corresponds to a period when resident black eagles in the Matobo study area increased from 54/55 to 61 territorial pairs (Gargett 1993 unpubl.: Table 6, p. 124). In fact, the correlation

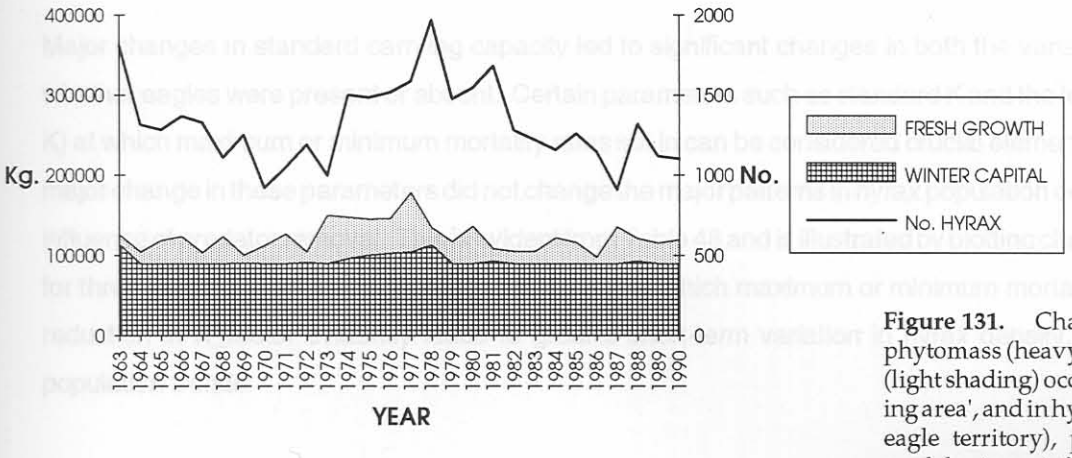



**Figure 131.** Changes in 'relevant' winter phytomass (heavy shading) and fresh growth (light shading) occurring within the 'safe feeding area', and in hyrax population density (per eagle territory), predicted by a run of the model using rainfall data for the Matobo Hills.

University of Pretoria etd – Davies, R A G (1994)



between predicted hyrax density in the Matobo study area (from the model) and the number of resident black eagle pairs in the Matobo study area (Gargett 1993 unpubl.) for the period 1963 - 1990 was statistically highly significant ($r=0,53$; $p<0,01$). Gargett's data (1993 unpubl.) on the change in eagle territories in the Matobo do indicate that black eagles are capable of a limited numeric response to changes in hyrax density. This is not catered for in the current model but ought to be considered in future modelling of the system. The breeding success (proportion of pairs monitored which raised chicks) of black eagles in the Matobo Hills for the same period (Gargett 1990: Table 34, p. 259; G. Banfield *in litt.*) did not correlate significantly with predictions from the model on hyrax density, but this parameter did correlate with the predicted number of surplus (P-K) hyrax in the eagle territories ($r=0,46$; $p=0,01$), and the predicted number of hyrax captured by the eagles ($r=0,42$; $p<0,05$). This supports the hypothesis that hyrax capture rate by black eagles is more influenced by hyrax availability than by hyrax abundance.

*Sensitivity analysis*

The main purpose of this model was to examine predation as a demographic factor affecting rock hyrax population change. The model predicts a very dramatic effect on the variance and size of hyrax populations when eagles are removed or predators are impeded. To test how robust this prediction is, the effect of removing eagles was examined for multiple runs of the model when individual parameters used in the workings of the model were varied dramatically. Parameters were increased or decreased by at least 50% where possible. But sometimes this was inappropriate (e.g. the heavy compensatory mortality rates due to starvation and disease set at 0,75), and was reduced to avoid extinction. In some cases, parameters such as standard carrying capacity could not be varied sensibly without covariance of another parameter (winter capital in this case).

To test the general robustness of the model, differences between the results of these runs and appropriate standard runs of the model (eagles present or absent) were assessed using three statistical tests: the F-test to detect differences in variation of population density; the normal test to detect differences in mean population density; and the Smirnov test to detect differences in the distribution of population density values. The results of these tests and examinations are presented in Table 48, and the conditions of parameter manipulation are described therein.

Major changes in standard carrying capacity led to significant changes in both the variation and density of hyrax whether eagles were present or absent. Certain parameters such as standard K and the levels (difference of P from K) at which maximum or minimum mortality rates set in can be considered crucial elements in the model. But even major change in these parameters did not change the major patterns in hyrax population density and in the predicted influence of predator removal. This is evident from Table 48 and is illustrated by plotting change in population density for three very different levels (known as K_factor) at which maximum or minimum mortality set in (Figure 132). A reduction in K_factor evidently leads to greater short-term variation in hyrax density, but the same long-term population trends.

University of Pretoria etd – Davies, R A G (1994)

# TABLE 48

## THE RESULTS OF A SENSITIVITY ANALYSIS PERFORMED ON THE MAIN PREDICTIONS OF THE HYRAX POPULATION MODEL

The principal effects of removing eagles (depletion of winter phytomass; overall increase in hyrax numbers; overall increase in the variability of hyrax population density; overall increase in the departure of P from K; and overall increase in hyrax surpluses) are listed for major perturbations of the important variables used in the population model. These perturbations are described under CONDITIONS. Predictions on hyrax population change for each perturbation were compared statistically to test for departure from patterns of hyrax population change predicted by the model under standard conditions. In each case, this was carried out for runs of the model with the full complement of predation and for runs of the model with eagles removed. Three statistical tests were used: the F-test to detect differences in variation; the Normal-Test to detect differences in mean population density; and the Smirnov-Test to detect differences in the distribution pattern of predicted hyrax densities. Asterixes denote where a statistically significant difference was obtained (two asterixes indicate P<0,01). The number of 'crashes' (when P > 4,5*K, and heavy compensatory mortality occurs) are also listed for each perturbation with and without eagles.

| | PRINCIPAL EFFECTS OF REMOVING EAGLES | | | | | Comparisons with appropriate standard runs of the model | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EAGLES PRESENT | | | | EAGLES ABSENT | | | |
| CONDITIONS | % REDUCTION OF PHYTOMASS | % INCREASE IN HYRAX NUMBERS | % INCREASE IN VARIABILITY (coefficient of variation) | INCREASED DEVIATION OF P FROM K | ADDITIONAL HYRAX SURPLUS | F-TEST | NORMAL TEST | SMIRNOV TEST | NO. CRASHES | NO. CRASHES | F-TEST | NORMAL TEST | SMIRNOV TEST |
| STANDARD RUN | | +32 | +6 | 1.53 | 622 | | | | 0 | 7 | | | |
| starting population halved | | +28 | +7 | 1.40 | 560 | | | | 0 | 7 | | | |
| starting population doubled | | +28 | +10 | 1.34 | 517 | | | | 0 | 8 | | | |
| initial phytomass down 30% | | +32 | +9 | 1.46 | 586 | | | | 0 | 7 | | | |
| initial phytomass up 30% | | +30 | +11 | 1.48 | 601 | | | | 0 | 7 | | | |
| edibility of winter phytomass doubled | -18 | +38 | +10 | 1.98 | 787 | | | | 0 | 6 | | * | |
| edibility of winter phytomass halved | -19 | +28 | +7 | 1.27 | 521 | * | | | 3 | 10 | * | | |
| phytomass constraints 50% wider | -35 | +7 | -18 | 1.19 | 412 | ** | | | 1 | 7 | ** | ** | ** |
| phytomass constraints 50% narrower | -8 | +46 | +25 | 1.66 | 757 | | | | 0 | 7 | | ** | * |
| levels for maximum mortality raised 43% | -17 | +53 | +13 | 2.04 | 1004 | | | | 0 | 7 | | ** | * |
| levels for maximum mortality lowered 43% | -14 | +14 | +4 | 1.06 | 248 | * | | | 2 | 10 | | ** | ** |
| phytomass 50% more sensitive to rain/herbivory | -15 | +36 | +21 | 1.48 | 628 | | | | 0 | 7 | | | |
| phytomass 50% less sensitive to rain/herbivory | -9 | +51 | +6 | 1.73 | 668 | ** | ** | ** | 1 | 7 | | | |
| standard carrying capacity up 50% | -14 | +16 | +4 | 1.29 | 599 | ** | ** | ** | 3 | 7 | ** | ** | ** |
| standard carrying capacity down 17% | -25 | +50 | -12 | 1.35 | 617 | | ** | ** | 0 | 7 | * | ** | ** |
| mortality rate during crash up 13% | -12 | +27 | +32 | 1.47 | 513 | | | | 0 | 7 | | | |
| mortality rate during crash down 13% | -17 | +38 | -1 | 1.61 | 698 | | | | 0 | 9 | | | |
| growth rate down by one third (phytomass up 50%) | -24 | +27 | +33 | 1.74 | 773 | | ** | ** | 0 | 6 | * | ** | |
| growth rate up by one third (phytomass down 25%) | -11 | +36 | +11 | 1.40 | 535 | | * | | 1 | 9 | | | |
| variability of pre-natal mortality doubled | -16 | +33 | +16 | 1.54 | 612 | | | | 0 | 8 | | | |
| variability of pre-natal mortality halved | -19 | +37 | +4 | 1.47 | 673 | | | | 0 | 5 | | | |

University of Pretoria etd – Davies, R A G (1994)



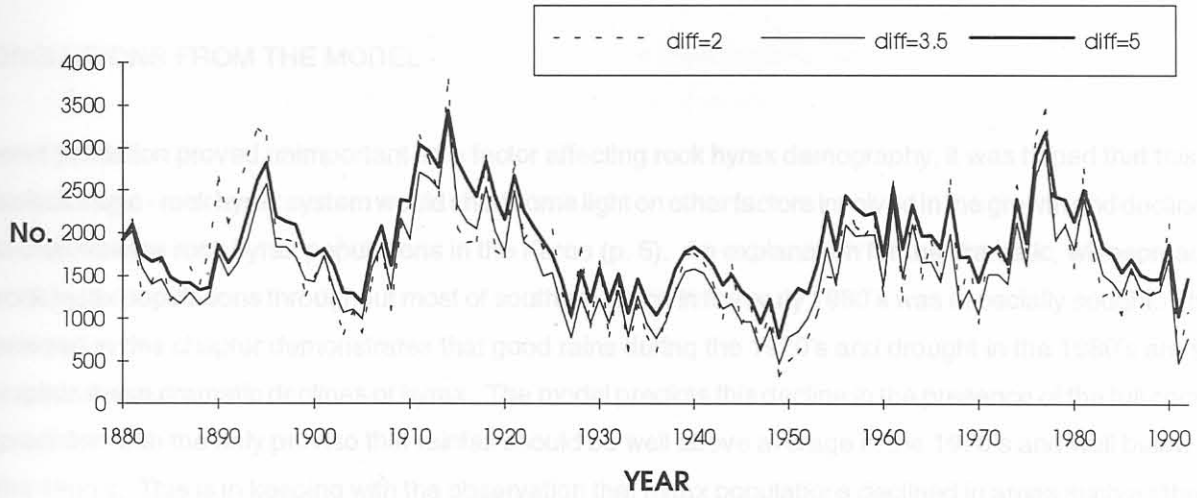



**Figure 132.** Predicted changes in hyrax population density for three variations of K_factor (the difference of P from K which invokes maximal or minimal values of mortality and fecundity) in the model (Beaufort West rainfall).

Parameter changes associated with increased variation in hyrax numbers were: an increase in standard K; a decrease in the edibility of winter capital (K primarily determined by erratic fresh growth); wider constraints on winter phytomass; and a lowering of the levels at which maximum or minimum mortality/conception rates set in. Increased variability in dynamic carrying capacity leads to increased variability of hyrax numbers as would be expected. Parameter changes identified as responsible for decline in mean population density were: lowering standard K; lowering winter capital and raising interest rates; and reduced sensitivity of phytomass to rainfall and herbivory. Widening the constraints on winter capital (allowing further depletion of phytomass by heavy hyrax consumption) did not lead to significant change in mean population density when compared with a standard run of the model with predators present. Discrepancy between observed and predicted hyrax densities during the study period might be explained by exaggeration of standard K in the model. But reducing standard K did not lead to a closer fit. Standard K in this model is based on accurate measurement of hyrax density in relation to the refuge environment, and there is no obvious reason why this should be over-estimated. As yet the discrepancy between the levels of observed and predicted values for population density during the study period remain unexplained.

Despite large perturbations of parameters in this analysis, the predicted effects of eagle removal on hyrax population density were remarkably consistent. Minor variation in the number of crashes (times when P exceeded K by 4,5) occurred, but the number of crashes was always much greater when eagles were removed. Inefficient tracking of K by P in the absence of eagles was represented by greater departure of P from K in all runs of the model. Consequently, an increase in hyrax surplus was predicted when eagles were removed for all parameter perturbations. This (average) increase varied between roughly 250 and 1000 hyrax per territory, but most perturbations indicated a similar increase to that under standard conditions (622 hyrax). Changing the P:K ratio level at which maximum/minimum mortality/conception rates set in had most bearing on the surplus of hyrax because this directly controlled the ability of P to track K. Hyrax surpluses in the absence of eagles were also affected (reduced) by widening of the constraints on phytomass. This results from further suppression of the phytomass and consequent reductions in hyrax densities in the absence of eagles. But both of these parameters that affect hyrax surpluses were based on inferences drawn from the observation of karoo biota and are not likely to be too far from real values. The sensitivity analysis indicates that impaired tracking of K by P in the absence of eagles (or impedance of predators) is robust for a wide range of parameter variation.

University of Pretoria etd – Davies, R A G (1994)



CONCLUSIONS FROM THE MODEL -

Even if predation proved unimportant as a factor affecting rock hyrax demography, it was hoped that this study of the black eagle - rock hyrax system would shed some light on other factors involved in the growth and decline phases that characterise rock hyrax populations in the Karoo (p. 5). An explanation for the dramatic, widespread decline in rock hyrax populations throughout most of southern Africa in the early 1980's was especially sought. The model presented in this chapter demonstrates that good rains during the 1970's and drought in the 1980's are sufficient to explain these dramatic declines of hyrax. The model predicts this decline in the presence of the full complement of predation with the only proviso that rainfall should be well above average in the 1970's and well below average in the 1980's. This is in keeping with the observation that hyrax populations declined in areas such as the Matobo Hills, where no predator control was in practice. Detailed analyses of rainfall patterns in the summer rainfall region over most of southern Africa have indeed revealed a particularly dramatic change from good rains in the 1970's to drought in the 1980's, and this change was also reflected in the population composition of hyrax captured by black eagles during the two decades.

A very simple lower trophic interaction in the model predicts that the food supplies and thus the carrying capacity for hyrax within the safe feeding area around rocky habitats shows phases of increase and decline due to the influences of rainfall and herbivory. These are closely followed by the hyrax population for a standard run of the model with predators present. Irruptions reported for hyrax populations in the Cape and Namibia correspond to decline phases in the model when shrinking food resources presumably forced the hyrax to become much more obvious (and vulnerable). This coincidence lends some support to the basic pattern of population change predicted by the model which remained robust despite dramatic parameter perturbation. Further supporting evidence for the basic model comes from fieldwork in the Matobo Hills where the predicted increase in hyrax during the 1970's and decline in the 1980's was mirrored by observed changes in the number of resident black eagle pairs, and from the KRNP where the predicted decline of hyrax in the early 1980's showed a strong correlation with hyrax counts at colonies. From very simple rainfall data, the model makes robust predictions about hyrax population change which concur with field observations.

So changes in food supplies and the number of hyrax that these can safely accommodate within the refuge environment can be considered to be the ultimate cause for the observed patterns of population change in a standard run of the model. The question remains as to whether the population changes are effected (proximate causes) primarily through the lower trophic interaction (e.g. through variation in numbers added to the population, and in numbers dying due to starvation), or primarily through the upper trophic interaction (through variation in numbers killed by predators), or by a combination of these effects. This can be explored either by key-factor analysis of population processes during a standard run of the model with predators present, or by simulating the removal of predation.

For a standard run of the model, mortality acting in the upper trophic level was calculated for each year as the number of hyrax killed by black eagles, plus the potential number of hyrax killed by caracals, plus 20% of the number of juveniles dying (the latter was taken to represent juvenile predation by small, generalist predators). Mortality acting

University of Pretoria etd – Davies, R A G (1994)



through the lower trophic level was calculated as the loss in breeding potential (described earlier) plus all remaining (non-violent) mortalities which are probably mostly caused by starvation, disease and possibly fighting. In a standard run of the model, population growth showed a significant negative correlation with mortality from above ($r=-0,80$; $p<0,01$), and an insignificant correlation with mortality from below ($r=-0,14$), suggesting that deaths due to predators can explain 64% of population change while losses due to the lower trophic level can explain only 2% of the change (conception rates were modelled on P:K ratio in these standard runs of the model, and not on stochastic rainfall patterns). Whether the population increases or declines is a function of both recruitment and mortality, but the results of this key factor analysis corroborate those of the field study which indicated that annual additions to the hyrax population are less varied and less involved in population change than annual removals by predators. But during the increase phase in hyrax numbers through the 1970's, population growth showed a stronger correlation with losses due to the lower trophic level ($r=-0,64$) while the relationship with predation remained unchanged. Variability in births appears to be partly involved in population change during growth phases. On the basis of these findings, I do not agree with the conclusion of other researches on karoo hyrax populations (Fourie 1983; Swart *et al.* 1986) that juvenile mortality is more involved than predation in hyrax population change, especially since the two cannot be separated.

It is important to note that rainfall influences both lower trophic losses and predation in opposite ways through food supply. This influence is destabilising to hyrax populations because good rains lead to increased recruitment and increased protection from predators, while drought leads to diminished recruitment and aggravated predation. This is supported by various lines of field evidence supplied in this thesis. Climate-induced destabilisation might be expected to have a far more dramatic influence on rock hyrax populations if these populations were not protected by a highly effective refuge resource when below the carrying capacity of this resource, and if these populations were not susceptible to very effective predation when above the carrying capacity of the refuge resource. The refuge resource of rock hyrax differs from most other forms of refuge in that it is effective against nearly all predators, and although food supplies in the vicinity of shelter may vary, the amount of rock crevices is not altered by climate or herbivory. Effectiveness of the hyrax refuge in this case probably prevents predation by specialist predators from destabilising the prey population, as it is known to do in other circumstances. The state of balance that exists between the food requirements of the hyrax population and the food supplies around the refuge habitat is apparently reflected in the distance that hyrax must venture from their rocks to feed, and thus in their vulnerability to predation. Some other prey populations may enjoy extra protection from predators when vegetation cover improves after rainfall, but most prey populations can be expected to become more available to predators as they become more abundant. The effectiveness of the refuge resource used by rock hyrax and the profound influence of enrichment on hyrax vulnerability are two key elements which appear to make this system rather unique amongst predator-prey relationships, and thus the present model must be regarded as specific.

The handling of hyrax capture rate by black eagles and especially by caracals in this model can best be described as 'availability-dependent'. The number of hyrax caught annually, as predicted by the model, was dependent on hyrax population density for both black eagles ($r=0,77$; $p<0,01$) and caracals ($r=0,43$; $p<0,01$) over a standard run of the model (112 years). However, there was no indication during a standard run of the model that predation rate (i.e. the proportion of the hyrax population removed) by black eagles or caracals behaved in a density-dependent

University of Pretoria etd – Davies, R A G (1994)



fashion, and this is more relevant to rock hyrax population change. Current demographic theory contends that if predation rate is not density-dependent then the predators cannot regulate the prey population (see earlier). Korpimäki (1993) reviewed definitions of population regulation and concluded from the disparity among these that it is a vague ecological concept: regulation has been strictly defined as 'the stabilisation of population density by density-dependent feedback mechanisms' (Solomon 1976; Kuno 1987), or 'the process whereby a population returns to equilibrium' (Nicholson 1933; Murdoch 1970; Sinclair 1989; Boutin 1992), and more leniently as 'long-term persistence and fluctuations within limits' (Mountford 1988; Hanski 1990; Messier 1991). I would argue that both key factor analysis (above) and simulated removal of predation (below) indicate that predation in this model does regulate hyrax populations in the lenient sense of the term - not around a simple equilibrium point, but around the number of hyrax that can be safely accommodated within the refuge habitat, and this number fluctuates primarily due to the stochastic influence of rainfall patterns. Large populations of hyrax may be safely accommodated within the refuge habitat during enrichment, while small hyrax populations may be exposed to predation during drought. Thus any long-term density-dependent trends in predation are obscured by short-term variation in the number of protected prey. This example illustrates that while density-dependent predation may still provide good evidence for regulation of prey by predators, the absence of density-dependence does not necessarily prove the contrary as is widely contended. Regulatory influence of predators may be less obvious in predator-prey systems which are complicated by variability in the number of protected prey. So variability in the number of red grouse protected by heather, in the number of voles protected by snow, or in the number of snowshoe hares protected by thickets ought to be considered before it is concluded that these prey are not regulated by predators on the grounds that predation was not clearly density-dependent. But safe and unsafe habitats are not likely to be more clearly defined than in the present system

Most of the above conclusions refer to predictions of the model when predators are present. Dramatic differences in hyrax population change when the model is used to simulate predator removal or impedance certainly corroborate the above indications that predation serves an important role in hyrax population change. Comparison of the patterns of population change with and without predators indicates that predation restricts departure of population density from the dynamic carrying capacity of the refuge habitat during enrichment, and especially assists its return during drought. The model indicates that the predation potential of black eagles and caracals has the capacity to remove the surpluses (P-K) of hyrax, even at high population densities assuming that these predation factors are realistically handled. Significant correlations between the breeding success of black eagles in the Matobo Hills and predictions from the model of the hyrax surpluses available to these eagles and the number of hyrax captured by these eagles, indicate that this is so. Predation of hyrax in the model is based on sound, biological field data for both black eagles and caracals. The dramatic influence of removing or impeding predation on hyrax population change indicates that variable hyrax birth rates and variable non-violent mortality rates as indicated during the present field study and from other lines of field evidence (and as handled under current assumptions of compensatory mortality) are evidently incapable at maintaining a close relationship between hyrax population density and changeable food supplies within the refuge habitat. This is despite the fact that both these parameters were modelled on P:K ratio thus affording opportunity for density-dependent effects.

University of Pretoria etd – Davies, R A G (1994)



By impairing the ability of the hyrax population to track the dynamic carrying capacity of the refuge habitat, it is predicted that predator removal or impedance gives rise to major peaks and crashes in hyrax populations, and to large surpluses of hyrax which will be forced to meet their forage requirements outside of the refuge habitat. On the basis that one adult sheep requires the same amount of food as 10 hyrax, it is estimated that the additional hyrax surpluses in the absence of black eagles would cost the average karoo farmer in mountainous terrain R3732 per annum (see methods). Low variability in the extra hyrax surplus predicted on removal of eagles for a wide range of dramatic parameter perturbations in the model (Table 48) indicates that this predicted cost is robust. Impedance of both eagles and caracals may be more appropriate for the karoo situation - just a 30% impedance of these predators may cost the farmer over R2700 in terms of grazing resources lost to increased hyrax surpluses. This extra cost may increase to nearly R7200 if predators are impeded by 70%, but high levels of predator impedance may be unrealistic for the simple assumptions on compensatory mortality in this model. These simulations did not involve impedance of small, generalist predators which may be responsible for a significant component of juvenile mortality. There was also no allowance in the model for colonisation of new habitats by hyrax in the absence of predators.

Unfortunately there are no good field data available to compare with these predictions, but it is likely that predator control was involved in major hyrax population increases reported in the Cape in the 1940's and on the farm Montana in the 1980's - these would not have been predicted by a standard run of the model with predators present. The validity of the predictions on the influence of predator removals rests mostly on the assumptions regarding compensatory mortality in this model. Undoubtedly these are a simplification of a complex phenomenon, but the object of the model was to capture the essence of this predator-prey system and the assumptions on the number of potential hyrax prey that would have died anyway due to old-age, starvation and disease were based on the limited field data available. Most support for the predictions is drawn from the sensitivity analysis performed on the model which demonstrated that increases in hyrax population density, variability and surpluses in the absence or impedance of predators all remained robust despite dramatic perturbation of even the most important parameters in the model.

The indications from the model presented in this chapter are that hyrax numbers change ultimately in response to changes in food supply within their refuge habitat, and that predation is essential for close tracking of these changes, although variable birth rates may also be involved during periods of enrichment and population growth. In this system, predation exerts an important regulating influence on a potentially unstable situation involving highly changeable food resources and a herbivore with a great propensity for population increase. Effectiveness of both refuge and predation contribute to population stability in rock hyrax, while alternating periods of enrichment and drought, and impedance of predation destabilise hyrax numbers. More information from field studies is still needed for the following aspects of this predator-prey system: the lower trophic interaction between rainfall, herbivory and karoo vegetation; the involvement of small, generalist predators in juvenile hyrax mortality; age-selective predation of rock hyrax by caracals; and, most important, the behaviour of non-violent mortality and compensatory mortality where predators are removed or impeded.

University of Pretoria etd – Davies, R A G (1994)



CHAPTER 13

# SYNTHESIS AND CONCLUSION

Much of the work covered in this thesis was collated and analysed in the previous chapter. The prime aim of this chapter is to answer the questions set out in the introduction which specifically pertain to the effect of black eagle predation on rock hyrax demography and the effect of black eagle predation on livestock in the Karoo. But before I do this I think it is necessary to briefly describe and contrast this predator-prey system with other systems, and the period of the present field study with others. Although only partly relevant to the demographic influence of black eagles on rock hyrax, I would also like to use this opportunity to draw conclusions on how black eagles may have influenced the 'lifestyle' of rock hyrax and *vice versa*.

*The system under investigation*

Despite a four-fold decline in hyrax numbers prior to the present study, rock hyrax were still the most important herbivores in the mountainous habitats of the KRNP. They are probably the most important competitors to domestic livestock for the veld resource in these habitats which occupy 15% of the Karoo. But the distribution of rock hyrax is clearly limited by that of their refuge resource. The fixed distribution of rocky habitats in the Karoo imposes a very real measure of 'K' or carrying capacity on this landscape for rock hyrax. Rock hyrax are extremely vulnerable to predators outside their refuge environment and may even be captured by humans on foot when found out in the open. Within their refuge environment, hyrax are extremely dextrous in their escape from predators, and rock crevices afford an effective refuge for hyrax from nearly all their predators (except possibly snakes). This refuge resource is unusual in comparison with other forms of refuge in predator-prey systems (e.g. snow and vegetation) because of its permanence and because of the high degree of protection it affords to an otherwise very vulnerable prey.

Although the degree of protection conferred upon the hyrax population is thus very clearly defined by rocks, evidence suggests that this parameter in the system is still variable. Hyrax must fulfil their food requirements by grazing or browsing vegetation growing outside the rock crevices. In the present study hyrax ventured farthest from shelter when they were foraging, and this was when eagles launched most of their hunting flights, made more of their strikes at prey and delivered more prey to nests. It appears that after enrichment of the system through rainfall, hyrax can achieve their food requirements at shorter distances from their crevices. After especially good rains, flushes of verdant green vegetation grow upon the nitrate-rich soils at the entrances to well-used rock crevices. During drought however, hyrax must forage further from the rocks and therefore they become more vulnerable to predators.

This deduction seems intuitive but it is also based on a few lines of field evidence: a negative correlation was established between the average distance moved from shelter by hyrax on 27 observation days at colonies and rainfall over the preceding 40d (although this correlation was not quite significant when one outlying observation was removed); time-lapse photography indicated that significantly more hyrax were delivered to black eagle nests in the dry year of 1988, and they comprised a larger portion of black eagle diet in the same year; the delivery rate of hyrax to black eagle nests apparently increased during dry spells and declined one to two weeks after rainfall events in

University of Pretoria etd – Davies, R A G (1994)



1987 and 1988 (but this could not be demonstrated statistically); bounty records also suggested a tendency that more hyrax were killed in dry years and fewer in wet years; these observations concur with the notion held by many karoo farmers that hyrax move far from their rocky shelters when stressed by drought (I actually observed this on the farm Montana in 1984); black eagle breeding success improved as conditions became dry, and declined as conditions became wet for all years that they were monitored in the Matobo Hills by Gargett (1990) prior to the early 1980's hyrax decline; eagle breeding success was also maximal in the present study during the dry year of 1988 (raptor breeding success is usually associated with food availability).

So while the area of safely-accessible vegetation around rocky habitats is fixed, the number of hyrax that this food resource can support appears to vary with rainfall. Greater protection afforded to hyrax after enrichment probably depends on the size of the rainfall event and the state of balance or imbalance between hyrax and their food resources. The phenomenon can be thought of as protection for a variable number of hyrax, but of course all hyrax will be influenced by the state of their food resources in the vicinity of shelter. Although increased vegetation cover after rains might confer some extra protection to prey in other systems, increases in prey abundance after enrichment are generally associated with increases in prey availability, and this is often reflected in correlations between rainfall and the reproductive rate of predators. Improved breeding success by black eagles during dry years rather than wet years is rather anomalous, especially for water-limited African environments, and suggests that variation in prey vulnerability may have more influence within this system than variation in prey abundance (at least on a year to year basis). So the black eagle-rock hyrax predator-prey system is characterised by a 'permanent' refuge resource which affords effective protection to a clearly-defined number of otherwise highly vulnerable prey, and this number varies in response to the influence of enrichment by rainfall. In the summer rainfall region of southern Africa, especially the Karoo, this rainfall is stochastic but shows some indication of long- and short-term cyclicity.

By reducing mortality rates affecting all hyrax age classes, and by encouraging very large birth-pulses, good rainfall events can have a very dramatic effect on rock hyrax population size and structure in the Karoo. The size of the birth pulses are most influenced by variation in conception rates, in precocious puberty of females and in pre-natal mortality. Each of these parameters is influenced by body condition, which depends on food, which in turn is affected by rainfall. Rainfall leading up to the birth-pulse explained nearly all the variation in hyrax recruitment in the present field study. But it is anticipated that crowding effects would have an influence on recruitment at higher hyrax densities. Heavy pre-natal mortality (possibly by abortion or resorption of foetuses) was suggested in the present study during very dry conditions in 1990, and has been noted in other studies of hyrax reproduction. Lactation might be impossible if the water content of the vegetation is very low, and termination of foetuses before birth would relieve female hyrax of this heavy burden. A sex-bias towards more male hyrax recruited in dry conditions was suggested by the frequency distribution of birth dates of male and female hyrax in both the large sample captured by eagles and the small sample collected by shooting (significantly so). Foetal sex ratio in the small shot sample did not differ significantly from parity but did lean heavily towards females (1,6 per male) in the wet year of 1989. It is not yet clear whether such a rainfall-related bias in recruitment of the sexes occurs before or after birth, nor how it might come about. If further research does not demonstrate a rainfall-related bias in foetal sex ratio, then the phenomenon is most likely explained by rainfall-related variation in predation risk operating on young dispersing male hyrax (during wet conditions most hyrax are well protected from predators and dispersers will be especially vulnerable). However, modelling did not indicate that this phenomenon would have a significant demographic effect.

University of Pretoria etd – Davies, R A G (1994)



So rainfall greatly influences the number of hyrax added to the population annually, and possibly the sex ratio of the first age class. The number of juveniles produced each birth-pulse and the number of these which survive their first year are important factors involved in rock hyrax population change, because of their great variability and because of the magnitude of the juvenile population component. As a result of rainfall effects, rock hyrax population structure is highly dynamic in the Karoo, and correlations were apparent between the age distributions of hyrax captured by black eagles and preceding rainfall patterns for the present study and for various other regions in the Cape Province sampled at different times. Variation in the size of adult hyrax skulls from prey remain collections also correlated with rainfall patterns both geographically and temporally, and not with vegetation type or temperature as has previously been suggested.

Overnight shelters must be in sufficient supply to accommodate the population increases of hyrax that are observed following good rains. Habitat mapping indicated that the average eagle territory in the KRNP contained over 44000 rock crevices available for use by the resident hyrax (about 63 groups). Hyrax population declines during drought suggest that safely-accessible food supplies in the vicinity of the refuge habitat set the local carrying capacity for hyrax, and not crevices for overnight shelter (which do not decline during drought). Hyrax groups were evenly spread through adequate rocky habitats in the KRNP but were often located close to riparian thickets and tended to cluster in kloofs where both food and shelter abounded. The fragmented and eroding rock outcrops of the Karoo appear to afford a surplus of rock crevices which can accommodate relatively high densities of rock hyrax. Foraging ranges of hyrax groups in the KRNP followed the distribution of rock outcrops, screes and riparian thickets, and within these ranges it appeared that suitable overnighting shelters were not in short supply. Suitable overnighting crevices may be more limiting in environments where the geology is not as suited to rock hyrax, but observations of hyrax in the Mackinder Valley in Kenya also indicated that the location of groups was more closely related to high quality food than high quality shelter (Sale 1965). For the Karoo at least, it appears justified to model hyrax demography on the amount of safely-accessible food around rocky habitat, rather than measures of overnight shelter.

As mentioned, hyrax in the KRNP as well as many other populations throughout southern Africa showed a significant decline in numbers during the early 1980's prior to the present study. The hyrax population in the KRNP declined further during the first years of field study. Detailed measurement of the refuge habitat and the frequency and foraging ranges of hyrax groups, indicated that hyrax were at 60% of their 'saturation level'. Hyrax were not using any temporary shelters for overnighting in the present study, as has been observed under high density conditions. Density estimates of hyrax in the present study were indeed much lower than those elsewhere in the Karoo and in Africa. It is indicated that the present study was carried out during conditions of unusually low hyrax abundance. Having declined by a factor of four, the hyrax population subsequently experienced several years of average rainfall and presumably average plant growth. One would expect the study population to be well protected within the confines of its refuge resource, and various lines of evidence did indicate a very low level of hyrax availability to resident predators:

Caracals used all habitats in the KRNP and probably occurred at a density intermediate between that recorded in the eastern Karoo and that in the south-west Cape (as indicated by trapping success rates). Despite this, caracals did not appear to be catching hyrax at all during the field study and instead, like true generalist predators, were relying

University of Pretoria etd – Davies, R A G (1994)


on alternate prey notably wild and domestic bovids. Black eagles were laying relatively small clutches and were breeding later than usual, except on farmland where they were making use of domestic lambs born and dying just prior to the eagle breeding season. Observations of foraging eagles indicated that they were putting more effort into hunting methods which were seldom observed in other studies. Success of strikes at prey and food provisioning rates at nests were much lower than has been observed elsewhere. Food provisioning rates did not vary with food need nor the hunting abilities of both parents suggesting a prevailing low level of foraging success. Provisioning rates by breeding eagles actually fell below the minimum food requirements estimated by metabolic predictions. Some eaglets had to survive nine days without food, and some eaglets probably died for reasons associated with low provisioning rates. Reduced food wastage through consumption of hyrax pelts and opening of hyrax crania occurred more frequently in situations where eagles were thought to be more food-stressed. It was estimated that black eagles removed 11% of the standing crop of hyrax annually, and this is lower than the average indicated by the literature for vertebrate predator-prey systems. Adult and old hyrax were seldom dying of any causes other than predation by black eagles except during the dry year of 1988. Black eagles were making use of the full range of prey species available, and may even have been removing 11% of the standing crop of a cryptic, nocturnal lagomorph, Smith's red rock rabbit. This prey species was evenly distributed throughout the mountainous habitats of the KRNP and comprised a convenient alternate prey for many eagle pairs. Pairs which took a large proportion of lagomorphs in their diet were able to achieve higher provisioning rates at nests. Unlike the predation of rock hyrax, variation in the predation of red rock rabbits closely reflected dramatic changes in the abundance of rabbits. These changes corresponded to rainfall patterns, but may also have been influenced by shifts in predation pressure caused by variation in the vulnerability of the dominant prey (in keeping with the alternate prey hypothesis). Over the entire field study, most lines of evidence indicated that hyrax were well protected within the confines of their refuge environment and relatively unavailable to resident predators. This should be borne in mind when interpreting the results of the present field study.

Black eagles occur at a high density in the KRNP, second only to the population in the Matobo Hills. The spacing of eagle nests along the upper escarpment in the park is the closest recorded along any linear mountain range so far. The high density of eagles can be attributed to the suitability of rocky habitats in the area which usually support relatively high densities of rock hyrax, and which afford the eagles with many tall cliffs for breeding. So the KRNP can be considered prime habitat for black eagles, and the population is probably limited by food rather than nest sites. The extent of eagle territories in the area was very closely related to the extent of prime hyrax habitat. Black eagles devoted slightly more time to defending their territories than to foraging, and the maintenance of territories is obviously essential for successful breeding. Black eagle territories have previously been considered very stable over time, and the possibility was considered in this thesis that eagles might use the distribution of rocky habitat as a cue for long-term indication of hyrax numbers. But rocks are of no use to the eagles when there are insufficient prey, and recent rather dramatic change in eagle territories in the Matobo Hills suggests that food is still the prime determinant of black eagle territory size where nest sites are not limiting. Despite low abundance and availability of hyrax during the present study, many eagles were still managing to raise chicks and the overall breeding success was not dissimilar to that recorded for the Matobo Hills population over a long period. Apart from the indications of low prey availability, the study population of eagles is not considered atypical for the species in good hyrax habitat, but black eagles elsewhere in the Karoo maybe more limited by the availability of nests sites.

University of Pretoria etd – Davies, R A G (1994)



There were consistent, detectable trends in the composition of black eagle diet from place to place and from time to time that were apparently related to hyrax:eagle ratios. Eagles in situations associated with a low hyrax:eagle ratio took many alternate prey and a small hyrax prey component in their diet amongst which females and juvenile hyrax were prevalent. Eagles in situations associated with a high hyrax:eagle ratio took few alternate prey and a large hyrax prey component in which males and old hyrax were prevalent. Eagles with many hyrax available to them can apparently fulfil their needs by preying on surplus elements of the hyrax population, whereas eagles with few hyrax available are forced to take more alternate prey and to prey upon healthy breeding stock amongst the hyrax population and more easily-captured but less profitable juveniles. A large portion of surplus prey elements such as males and old individuals in predator diet has been associated with high prey:predator ratios for hyenas preying on wildebeest in the Serengeti (Kruuk 1970, 1972a) and with inefficient predation upon ungulate prey populations during the Oligocene - more healthy young adult ungulates fell prey to the efficient predators of the Eocene (Bakker 1983). For black eagles this variation can apparently come about in one of three ways: certain pairs may inhabit mountain ranges where hyrax densities are low and hyrax:eagle ratios are low despite large hunting ranges (e.g. mountains in the Fynbos biome); certain pairs may experience low hyrax:eagle ratios after a significant decline in hyrax abundance; and certain pairs may experience an effective low hyrax:eagle ratio when good rains lead to reduced availability of hyrax. Variation in eagle diet between the 1970's and the 1980's in two regions of the Cape may have been caused by changes in both hyrax abundance and availability. In the present study black eagles nesting on the upper escarpment showed symptoms of low hyrax:eagle ratio which were probably related to both topography and changes in hyrax abundance. Consequently upper escarpment pairs did not breed as successfully as lower escarpment pairs (despite higher failure rates of the accessible lower escarpment nests), and suffered more territorial intrusions. The only advantages enjoyed by upper escarpment pairs were better flying and hunting conditions. Black eagles which occupy small territories in high density hyrax habitat (e.g. Matobo Hills; upper escarpment) are probably more susceptible to instabilities in the hyrax prey base, and this might explain recent, quite dramatic territory changes among black eagles in the Matobo Hills following a hyrax decline (Gargett 1993 unpubl.).

*Links between the lifestyles of black eagles and rock hyrax*

Despite relatively low prey:predator ratios inferred during the present study, rock hyrax still comprised the principal food of black eagles as indicated by a variety of methods. So, unlike the generalist caracals, black eagles were behaving as specialist predators of rock hyrax by pursuing their preferred prey at low density and low availability. There was no indication that black eagles 'switched' to other prey in response to changes in their abundance (but it is unlikely that suitable alternate prey were in sufficient supply within eagle territories to invoke such responses). Specialist predation on rock hyrax by black eagles was also apparent when comparing black eagle diet with that of martial eagles resident in the area. Rock hyrax have dominated black eagle prey in nearly every study of black eagle diet. Comparison of methodology in the present study indicated that this dominance is significantly exaggerated in most studies where collections of prey remains are analysed, and small lagomorph prey are consistently under-estimated by this technique. Nevertheless, a heavy reliance on rock hyrax is indicated for black eagles wherever they occur in Africa.

University of Pretoria etd – Davies, R A G (1994)



Specialist predation by black eagles exerts hard selection upon adult hyrax. During the present study, it was estimated that approximately three out of four deaths of adult and old rock hyrax were caused by black eagles. In the presence of such strong selective pressure operating on reproductively-active adult hyrax, morphological or behavioural adaptations that enable hyrax to evade predation by eagles should accumulate in the population. Bakker (1983) estimated that only one death per 100 - 1000 in each generation (5y) was necessary to cause the observed evolution of cursorial limbs among mesonychid predators and their prey over a 15 million year period. Bakker maintained that this very weak overall level of selection (by standards of animal breeders) would not be swamped by random genetic events because the rate of selection was not gradual and short periods of heavy selection are likely to have occurred in between long periods of stasis. Some authors have suggested that coevolution between predators and prey should result in prey populations that are highly productive and, consequently, a high ratio of consumers to producers (Allen 1976). Others have argued the exact opposite (Ives & Dobson 1987). There are many factors involved in the crop of rock hyrax removed by black eagles and in the overall ratio of hyrax to eagles as already described. These parameters are also subject to limitations characteristic of populations of warm-blooded vertebrates, so I do not think they give any indication of the likelihood that coevolution has arisen in this system. Previous coevolution between black eagles and rock hyrax can be considered likely because of the heavy reliance of black eagles on this prey for food (indicated by all studies) and thus for successful breeding; and because of the hard selection exerted upon reproductively active rock hyrax by black eagles as evidenced in the present study. It is possible that both species may have been extant for the last 25 million years. Coevolution would be inevitable if these conditions of the predator-prey relationship had been operating over such a period. However, it should be noted that while black eagles appear to rely on hyrax throughout their range, rock hyrax must face other threats besides black eagles, especially as juveniles, especially at high densities, and especially in regions where black eagles may be nest-site limited or absent.

Coevolution requires specificity and reciprocity, and is usually taken to mean 'that a trait of one species has evolved in response to a trait of another species, which trait itself has evolved in response to the trait in the first' (Futuyma & Slatkin 1983: p. 1). In the following section the possible occurrence of coevolution between black eagles and rock hyrax is considered by comparing their functional morphology and ethology. As Futuyma & Slatkin (1983: p. 10) state: "Careful analysis of unusual or unique characters of each of two interacting species can show these features are one species' adaptations to the other species. This evidence is indirect and often not conclusive but may be the only kind available".

Identifying morphological features that may have resulted from coevolution in this system is difficult because many of the adaptations that assist black eagles to catch rock hyrax, or that assist rock hyrax to evade black eagles can also be considered as adaptations to the rocky, mountainous habitats in which they live. The stout build, low centre of gravity, thermal lability and rubber-like soles of rock hyrax are some of the numerous adaptations that enable this species to successfully exploit rocky environments (Sale 1970a). The high aspect-ratio wing 'design' of black eagles enables them to make good use of the slope lift over mountains. These morphological features can disadvantage the animals outside of their natural habitat - hyrax are especially vulnerable to predators away from rocky shelter, and black eagles do not soar as efficiently as other eagle species on thermals over plains. These pressures are likely to have reinforced their mountain lifestyles.

University of Pretoria etd – Davies, R A G (1994)



Certain morphological features of rock hyrax provide advantages against all predators, such as their cryptic coloration. Sale (1970a) argued that the dorsal spot of *Procavia capensis* is not strikingly coloured because these animals inhabit areas of low predation pressure where a visual alarm signal is not needed. As the present study indicates, there is very strong predation pressure affecting *P. capensis*, perhaps even more so than in East Africa and especially West Africa where black eagles are absent. I believe that the auditory alarm signals employed by *P. capensis* are far more effective than any visual signals, and that the dorsal spot is used to signal intention to conspecifics (pers. obs.). I think Sale's argument should be inverted - that *P. capensis* has a cryptic dorsal spot because of **high** predation pressure. The only morphological feature of rock hyrax that might be attributed to the evolutionary influence of an avian predator is the adjustable umbulacrum of the iris - it has been suggested (Millar 1971) that this structure might enable rock hyrax to detect eagles making strikes with the sun behind them (a behaviour that was observed in the present study). The absence of such a structure in eyes of *Procavia* spp. from West Africa where black eagles are absent, would be strong supporting evidence for this hypothesis.

Black eagles in the present study fed mainly on immature and adult rock hyrax. Full-grown hyrax are formidable prey. Despite the fact that golden eagles hold most of the records for largest prey killed by eagles (Table 26 - this may be because golden eagles have received most attention), mean prey size killed by black eagles in the present study was more than twice that recorded in two golden eagle studies. I suggest that the large foot dimensions of black eagles, which are considerably larger than any other *Aquila* spp. (including the golden eagle which is 14% larger than the black eagle by mass), have been selected for the hunting of large hyrax prey. Male black eagles have particularly large feet (almost as large as female feet) for their body size, and I suggest that this is due to the fact that pairs of black eagles hunt cooperatively for the same large hyrax prey.

Predation may also have an influence on the breeding biology of rock hyrax and black eagles. High predation pressure (from all predators) may explain why rock hyrax show a distinct birth pulse in an unpredictable climate. Black eagle nestlings fledged immediately prior to the modal hyrax parturition date, affording the young eaglets an abundance of available prey. Similar timing of fledging has been observed for other raptor species (Olsen & Georges 1993). But there is also some indication that black eagle nesting seasons throughout the continent may be timed to coincide with high hyrax availability during the dry season (see Moreau 1950).

Moving on to behaviour, the risk of predation to a hyrax living in an average black eagle territory in the KRNP was 0,03% $day^{-1}$. This is comparable to the risks incurred during racing car driving for humans. Rock hyrax showed two principal behavioural lifestyle characteristics which minimise these risks: 98% of the population lived in groups; and the entire population lived in a refuge environment. Both these characteristics have other advantages besides reducing predation risk, but tolerance of sexually-quiescent adult male hyrax within harem groups (suggested in the present study and confirmed in other studies) indicates that maintenance of adequate group size might be more important than strict social organisation. Disappearance and coalescence of small hyrax groups in 1988 indicates that these small groups may have suffered very high predation pressure through lower vigilance. Large groups benefit from increased vigilance, and rock hyrax posted obvious sentinels (mainly old females) when group-foraging to give early warnings of predator attacks. Dispersing hyrax (mainly immature males) are known to reduce the risks of predation by moving through non-rocky terrain at night, but may find themselves in risky situations during the day.

University of Pretoria etd – Davies, R A G (1994)



Immature males and old females were the most highly preferred hyrax prey of black eagles in the present study. Young dispersing male hyrax probably become vulnerable to eagles when moving away from familiar terrain without the group benefits of vigilance and sentinels. Sentinels probably run the risk of eagle attack when hurrying to catch up with foraging groups. Perhaps on account of low hyrax availability, black eagles preferred to first sight their prey from a perch or a high altitude flight and then plan their approach which usually involved some use of cover to maximise the element of surprise and delay early warnings by their intended prey. This technique differed from that described in the Matobo Hills (Gargett 1990) where black eagles appeared to fly more randomly around rock outcrops and surprise hyrax in passing, apparently without previously sighting their prey and planning their approach.

Black eagles can detect rock hyrax from at least two kilometres distance and make hidden approaches to their prey at speeds which are 4-10 times faster than the maximum escape speed of rock hyrax. It cannot be said that there is much 'adaptive gap' between this predator and its prey. The early warning system employed by foraging hyrax requires immediate access to refuge in the presence of such highly mobile predators. Hyrax spent 96% of their time within 5m of a bolt hole and did not forage farther than 15m from their rocks - this was reflected in a distinct vegetation zone around well-used outcrops. It is suggested that the apparent cut-off point at 15m from shelter is the product of a trade-off between foraging return and risk of predation. Eagles and other predators evidently exert a strong behavioural as well as numeric influence on hyrax populations. In a fast glide, black eagles travel at four times the maximum speed of hyrax, so the reluctance of hyrax to venture beyond 15m suggests that in the topography of the KRNP black eagles are probably able to conceal most attacks until about 60m from their intended prey. By similar reasoning, relaxed behaviour of hyrax when they are within 5m of shelter suggests that eagles find it difficult to remain undetected until within 20m of their intended prey. These safe and unsafe zones probably depend on topography and eagle:hyrax ratios (likelihood of attacks). Hyrax effectively minimise time spent away from their rocks by conducting casual feeding in the immediate vicinity of rock outcrops and by making extremely efficient use of their time on group foraging bouts while they access better quality vegetation: for one to two hours on most days hyrax groups engaged in intense bouts of feeding, usually in riparian thicket, sometimes 500m from their colony rocks; foraging groups were highly mobile through the network of linear outcrops, screes, and thickets, and appeared to actively harvest or garden different parts of riparian thicket on consecutive days.

Many raptors attacking prey, such as eagles attacking lagomorphs, miss on their first strike and often only secure their prey on a second or third attempt. For a prey species which spends 96% of its time within 5m of a bolt-hole, the chances of a second strike are minimal. I suggest that the prevalence of tandem behaviour in black eagles has arisen through the advantages of cooperative hunting as a means of capturing elusive rock hyrax. Tandem attacks at prey were nearly twice as successful as solo attacks (although this difference was not statistically significant), and the eagles probably only experience a limited number of attack opportunities each day. Black eagles spent 80% of their hunting time together and in close contact. Tandem hunting by black eagles fulfilled most of the requirements for true cooperative hunting, and the division of labour employed by eagle pairs during an attack could be related to the dimorphic capabilities of the sexes.

Certain links could be established between the foraging behaviour of hyrax and eagles. Coincidence of black eagle and rock hyrax daily foraging rhythms on an overall, seasonal basis suggests that eagles are mostly able to predict

University of Pretoria etd – Davies, R A G (1994)



hyrax availability in time and adjust their own activity accordingly. This is probably because hyrax face certain daily limitations on how they use their time, such as the need to spend the mornings sunning during winter, and the need to avoid midday heat in summer. However, hyrax were apparently able to avoid high risk periods in the short-term and did not venture on group foraging bouts on windy days when eagles were more active (and delivered significantly more prey to their nests).

Rock hyrax populations in the Karoo show obvious population fluctuations related to rainfall. But hyrax can be very obvious animals and habitat shift and dispersion during drought may have been perceived as the population 'explosions' reported in the literature. Even during the 'dramatic' decline in the early 1980's hyrax numbers in the KRNP only varied by a factor of four. Hyrax populations on Serengeti koppies, monitored for 17 years by Hoeck (1989) did not show more than a four-fold variation in numbers (only two-fold for *Procavia*). More typical eagle prey such as lagomorphs show far greater variation in numbers than this. Even red rock rabbits during the present study showed a ten-fold variation, and that was not noticed by most observers in the KRNP. It is quite common for lagomorphs to show a 30-fold variation in numbers (Caro & FitzGibbon 1992). Rabbits in Australia and smaller raptor prey elsewhere can show even greater population variation than this e.g. vole numbers can vary by a factor of 100 (Korpimäki 1986; Norrdahl 1990), and lemming numbers can vary by a factor of 1000 (Maclean *et al.* 1974). The low variability of hyrax numbers makes this a very unusual prey for raptors. Lagomorph numbers vary far more than hyrax numbers because lagomorphs have a greater potential for population increase and they are rarely limited or protected by a permanent refuge resource. Unlike vulnerable hyrax, lagomorphs may sometimes escape the local predation capacity.

Relatively stable and high densities of rock hyrax have permitted black eagles to become highly prey-specific and to nest at unusually high densities for such a large eagle species. Because they nest relatively close together, black eagles have evolved spacing behaviour based on visual cues. They are highly conspicuous birds, especially in their undulation display. Most mountainous habitat in Africa appears to be saturated with black eagle breeding territories. Black eagles are long-lived, so the chances of juvenile eagles surviving to adulthood and establishing themselves in these breeding territories are very small. Simmons (1988, 1991) argues that this selection operating against young black eagles has led to conservative reproductive behaviour, involving obligate siblicide, which tends to produce high quality and competitive offspring. I would like to add to this argument the influence of a stable hyrax prey base which can be expected to encourage stable black eagle territories. Breeding opportunities for immature black eagles are probably more hard to come by than breeding opportunities for other immature *Aquila* eagles in environments where prey bases are much more variable and where harsh climates may cause eagle mortalities. So many facets of black eagle lifestyle can be related to a high degree of stability which is resonant in this predator-prey system, and which is created primarily by the fixed extent and the effectiveness of the rocky refuges used by hyrax.

*Do black eagles limit rock hyrax populations in the Karoo?*

Unlike the evolutionary influence of black eagles upon rock hyrax, their demographic influence could be directly measured in this study. The field study indicated that the number of hyrax removed from the prey population annually was equivalent to nearly one third of the numbers added annually. Many of the hyrax removed by black eagles

University of Pretoria etd – Davies, R A G (1994)



belonged to age classes (e.g. adults) which suffered low mortality to factors other than eagles, so only a minority of these unfortunate individuals were likely to have died in a given year if they had not been captured. This was especially the case for hyrax captured in upper escarpment eagle territories where prey:predator ratio was low and the eagles were preying extensively upon apparently healthy breeding stock. It is concluded that during the present study much predation of rock hyrax by black eagles comprised additive rather than compensatory mortality. By removing a significant number of hyrax from the population which were otherwise unlikely to have died, it can be said that black eagles did have a limiting influence on their prey during the field study. This is easy to state given the broad definition of a limiting factor as any factor which affects population growth through increased production or loss of individuals (p. 254), and the conclusion that black eagles can limit rock hyrax actually tells us little about their long-term influence on hyrax population density in the Karoo. This is best explored by key-factors analyses and modelling.

*Were hyrax 'irruptions' in southern Africa caused by the removal of predators?*

First, the field evidence does not suggest that rock hyrax populations can usually be described as irruptive or epidemic. Many reports that hyrax populations reached 'plague' proportions in the past were probably over-stated. The rock hyrax population in the KRNP at the start of the 1980's was described as such and there were eye-witness accounts of 'hillsides teeming with dassies', yet counts in the park indicated that the population subsequently only declined by a factor of four (Fairall 1991; *in litt.*) to the low levels observed in the present study. This represents an extremely low level of population variation when compared with populations of other medium-sized eagle prey such as lagomorphs. Rock hyrax are very obvious diurnal animals, and I think it is likely that habitat shift (moving far from rocky outcrops to feed) and dispersal (to colonise sub-optimal refuge habitat) made them even more obvious at times when the populations were stressed, giving rise to the perception of sudden population 'explosions' or plagues. Reports of these phenomena actually coincided with predictions from the hyrax population model of major decline phases, as would be anticipated, when large hyrax populations were stressed by drought. So I think much of the perception of hyrax population irruptions was actually caused by a greater noticeability of the animals due to behaviour change, and this is in keeping with the many lines of evidence listed earlier which indicated that hyrax become more available to their predators in dry years when vegetation deteriorates. Population 'eruptions' (moving out) is probably a more fitting term for these situations than population irruptions (moving in).

All-said, there is little doubt that hyrax populations throughout southern Africa were at a peak at the end of the 1970's and many showed a subsequent decline to maybe a quarter of their former numbers during the 1980's. The observation that this dramatic population change occurred in the Matobo Hills where predators were not persecuted, concurs with the observation that the same order of change is predicted by the hyrax population model in the presence of the full complement of predation. In fact, a very different order of change is predicted in the absence of predators, because predation is apparently an important facilitator for the decline phase. It is clear that hyrax populations rise and fall fairly dramatically without any interference by predator removals, and it is inferred that the apparent 1980's hyrax population eruption was not caused by predator removals.

University of Pretoria etd – Davies, R A G (1994)



So what are the 'eruptions', and the increase and decline phases that characterise rock hyrax populations caused by? A relatively simple, but specific population model for rock hyrax predicts that these phases can be adequately explained simply in terms of rainfall patterns and concordant change in the food supplies available to hyrax in the vicinity of rocky habitat. In this model it is assumed that hyrax mortality (including predation) and recruitment rates, both based on field data, are determined by the state of balance between the hyrax population and food supplies in the vicinity of rocky habitat. The predation response is thus modelled not on the ratio of prey to predators but on the ratio between prey and their own food resources. The food supplies, in turn, are modelled on the relationship between plant production and rainfall which has been observed for arid and semi-arid rangelands. When it is assumed that the base for plant growth is fixed from year to year, the model predicts erratic change in food supplies and hyrax numbers. But when plant production is modelled as the rainfall-determined interest (annual fresh growth) on a capital (winter phytomass) that is allowed to increase in years of good rains and light herbivory, and to decline in years of drought and heavy herbivory (within realistic limits), then the model predicts more gradual increase and decline phases for the hyrax population, the most recent of which showed strong agreement with field observations from both the KRNP and the Matobo Hills. Three previous declines (when phytomass was suppressed to its lower limit) were predicted at times when hyrax eruptions were reported in the literature. These predictions of the model were robust for a wide range of dramatic parameter perturbations.

The increase phases of the hyrax population occur when good rains and improved food supplies lead to both reduced mortality and increased recruitment. Reduced mortality at such times can be attributed to better protection from predators and reduced competition for food supplies which can be expected to lead to improved body condition and less fighting. If conditions are optimal then major birth pulses are likely resulting in extremely large populations. It appears that this build-up phase in the hyrax population may pass unnoticed by human observers, presumably because the animals can obtain all their food requirements in the vicinity of their rocky habitat. If such large hyrax populations enter a period of drought, then shrinking food supplies in the vicinity of the rocky habitat can be expected to cause a decline through reduced recruitment and aggravated mortality (for reasons opposite to those listed above). In this way alternating periods of enrichment and drought (which characterise the Karoo) have the effect of destabilising hyrax numbers. Such climate-induced destabilisation might be expected to have a far more dramatic influence on hyrax populations if these populations were not protected so effectively by a refuge resource when below the carrying capacity of this resource (set by food supplies in the vicinity of rocky habitat), and if these populations were not susceptible to such efficient predation when above the carrying capacity. In this context, predation of rock hyrax differs from what has been described as 'environmentally-modulated predation' for Australian situations where prey species such as rabbits can escape the local predation capacity when conditions for population growth are optimal. Climate-induced destabilisation of hyrax populations can be expected to be greater in regions where climate is more variable and less predictable. It is relevant to note that major hyrax eruptions have only been recorded in the arid summer-rainfall areas of the Karoo and southern Namibia where rainfall is more stochastic and droughts are more severe.

The model predicts that major enrichment followed by major drought are both necessary to cause a dramatic hyrax decline, as observed in the early 1980's. Simultaneous dramatic declines of other ungulates suggest that elements in the lower trophic model (although simplistic and based on minimal field evidence) may find wider application for

University of Pretoria etd – Davies, R A G (1994)


vegetation-herbivore interactions. Large hyrax populations may suffer heavy predation and decline when conditions are dry for a year, but the major eruptions were only reported after three to seven years of drought following enrichment. This suggests that total pasture exhaustion is necessary for dramatic alteration of hyrax behaviour and the invasion of new habitat. The reported eruptions also showed some coincidence with the timing of 'treks' by springbok in the arid zone (see Skinner 1993). These treks also involve dramatic behaviour change and have been linked to pasture deterioration.

It is likely that all the reported eruptions were caused by such pasture exhaustion, except possibly for the 1940's eruption. Only minor increase and decline phases are predicted for this period by the model whether based on Beaufort West, Stolshoek or district rainfall, and this is not in keeping with Thomas' (1946) observations that hyrax in the Cape midlands had recently increased enormously in numbers and had overflowed from the rocky habitats onto the plains. Construction of jackal-proof fences had been completed and destruction of predators had been very intense over the preceding 10 - 15 years, so it would appear that the 'magnitude' of this reported eruption may owe more to predator removals than to climate. The severe drought at that time may have forced the hyrax to invade new habitat, but predators were probably insufficient to remove these surplus animals. It is possible that a similar scenario was involved in the hyrax eruption reported for Namibia in the late 1960's. The unexpected recovery of hyrax on the farm Montana where caracals and secondary predators were heavily persecuted also indicates that interference with predators may alter the natural pattern of hyrax population change. To conclude, increase and decline phases in hyrax populations are naturally caused by changes in their food supplies in the vicinity of rocky habitats, and may result in major eruptions when large hyrax populations experience extended drought and pasture exhaustion. This pattern may be altered, and eruptions may be 'aggravated' by the removal of predators.

*Do black eagles regulate hyrax populations in the Karoo?*

A potentially unstable situation exists when a prey species with a very high propensity for population increase experiences a changeable food supply. In Australia for instance, this type of situation has led to massive irruptions of rabbits. If hyrax numbers follow changes in their food supplies in the vicinity of rocky habitat, it is important to know whether the change in hyrax numbers is brought about through the upper trophic level (mortality due to predators) or through the lower trophic level (loss of breeding potential and starvation), i.e. what are the proximate factors causing population change? Key factors analysis performed on population change during the short field study indicated stronger correlations with predation than with lower trophic factors. Although birth pulses varied greatly in the field study they were more related to rainfall patterns and they only affect the first age class, whereas predation affects all 12 age classes. The implication was that losses through the upper trophic level were more varied and more involved in hyrax population change than losses through the lower trophic level. However this result was likely to be influenced by conditions during the short field study. To escape these limitations, key factor analysis was conducted on a full run of the population model (over 112 years), in which the limits of demographic factors had been set in accordance with a variety of field studies. This analysis indicated that upper trophic losses could explain most population change and lower trophic losses a negligible amount. Despite the magnitude of variable hyrax birth pulses, this demographic factor appears to have more influence on hyrax population structure than on population

University of Pretoria etd – Davies, R A G (1994)


size. The only time lower trophic losses appeared to be partly involved in population change was during periods of enrichment when large birth pulses facilitated growth. Predators appear to be essential for facilitating population declines when food supplies shrink. This tallies with observations on cyclic prey, where predators appear to be more involved with the decline phase than with the increase phase. One implication of this is that predator removal experiments conducted during enrichment are likely to yield very different results from predator removal experiments conducted during drought.

With the full complement of predators, the model predicts that hyrax populations are able to closely track changes in the carrying capacity of their refuge resource set by food supplies. Indications of the key factor analyses that predation is mostly involved in this close tracking were supported by simulating predator removals. Simulated removal of eagles or relatively low impedance of both eagles and caracals resulted in increased hyrax population density and large surpluses which regularly invoked heavy compensatory mortality when the population greatly exceeded the carrying capacity. A similar increase in the frequency of brown locust 'outbreaks' in the Karoo has also been attributed to the removal of natural predators (Hockey 1988). A much more significant increase in hyrax numbers was predicted for the 1940's with removal of eagles or >30% impedance of both major predators. The increased propensity for hyrax population growth under these simulations was so great that the model predicted increase phases when the population would naturally be declining. The predicted chain of events in the absence of eagles was robust for a wide range of dramatic parameter perturbations. Losses through the lower trophic level (variable birth rates and non-violent mortality rates) were based on field data and modelled on the ratio of hyrax food need to hyrax food supply, but they were evidently not sufficiently variable to ensure close tracking of food supplies by the hyrax population. Whereas the local predation response, also based on extensive field research, had the capacity to annually remove hyrax surpluses as they arose (even at high densities).

The black eagle - rock hyrax system shows some similarities to other predator-prey systems. Like other prey populations, hyrax populations rise and fall intermittently and predators play a key role during rapid decline phases. But these phases are not regular as for cyclic prey - they correspond to periods of enrichment and drought like the environmentally-modulated systems of Australia. But unlike the Australian systems, hyrax populations do not under natural conditions escape the capacity of the local predation response, and they enjoy effective protection from predators when their food requirements can be met within their refuge environment. Consequently the order of magnitude variation in hyrax numbers is far lower than that recorded in other cyclic or environmentally-modulated systems. Enhanced stability of rock hyrax populations in comparison to other prey can be attributed to three main factors: a fixed area of refuge habitat; the effectiveness of this refuge against nearly all hyrax predators; and high vulnerability of hyrax to numerous and efficient predators outside of their refuge environment. Rock hyrax are also unusual when compared with other prey because they become less available, despite increased abundance during enrichment, and more available despite decreased abundance during drought. The black eagle - rock hyrax system may be described as a 'refuge-mediated' predator-prey system which can be destabilised to a limited degree by climate.

Predators clearly ensure close tracking of food supplies within rocky habitat by hyrax populations. They do this by efficient removal of surplus animals. Does this mean that the predators are regulating hyrax numbers? No density-

University of Pretoria etd – Davies, R A G (1994)



dependence could be found for the predation response in the field study or in a standard run of the model. In accordance with current demographic theory it would appear that this predation does not fulfil the strict definition of a regulating factor as: 'the process whereby a population returns to equilibrium'. But hyrax populations are unusual in that large populations may be protected from predators in wet years while small populations may be exposed to predators in dry years. This annual variation in the number of protected prey is likely to have hidden any density-dependence in the predation response. Population regulation has been defined in a more lenient sense as 'long-term persistence and fluctuations within limits'. I believe that the predators of rock hyrax, by efficient removal of surplus animals, do regulate hyrax populations in this sense of the term, between long-term limits that are defined by minimum and maximum food supplies within the well-defined patches of refuge habitat.

As to the question of whether black eagles, specifically, regulate hyrax populations in the Karoo, this would appear unlikely. In the model, predation by black eagles was free to compensate when caracals were impeded by 50%, yet the predation response of the eagles did not have sufficient capacity to prevent departure of the hyrax population from its carrying capacity. Black eagles (two pairs) on the farm Montana were apparently unable to prevent a hyrax population increase which was attributed to destruction of caracals and secondary predators of hyrax. Yet simulated removal of eagles in the hyrax population model did have a very dramatic effect on hyrax population change (this effect might be somewhat reduced in real situations where caracals may compensate). I would conclude that black eagles are not the sole agent responsible for regulation of hyrax populations, but that black eagles, caracals and the secondary predators of juvenile hyrax are all essential ingredients for an efficient predation response which can regulate hyrax populations about the changing carrying capacity of the refuge environment. Rather than reaching an equilibrium with their prey, these predators have the effect of maintaining an equilibrium in the lower trophic level within the refuge environment.

Most specialist predators have a destabilising influence on their prey due to time-lags in their numeric responses, and by pursuing their prey at low density. Black eagles were indeed catching hyrax despite very low prey availability, but at an apparently reduced rate. Destabilisation of rock hyrax populations by specialist black eagles (in the generation of regular cycles) is prevented by limitations on any numeric response by black eagles, and by the high degree of protection afforded to hyrax populations when their food need can easily be met by food supplies within the refuge environment. The model did not indicate much difference between the demographic influence of specialist predation by black eagles and generalist predation by caracals upon the hyrax population. It was anticipated that more consistent predation by eagles might have more influence during enrichment, while caracals would have a greater capacity for removing large surpluses in drought. However, interactive effects were probably not properly handled in the model to draw any conclusions on this matter. Field evidence suggests that the emphasis of age-specific predation upon hyrax by black eagles might change with prey:predator ratio, but the model did not indicate that this would be of great demographic significance.

The system under investigation is unusual as a refuge-mediated predator-prey system for the reasons given above, and the hyrax population model evolved in this thesis must be viewed as specific to this situation. Nevertheless the results of this investigation may find some application in other systems. The lower trophic interaction is simulated in the model in a very simple fashion based on changeable 'plant capital and interest', yet the predictions agree with

University of Pretoria etd – Davies, R A G (1994)


field data and may be used to explain synchronous declines in ungulate populations in the early 1980's. Much still needs to be learned about the effects of rainfall on vegetation - herbivore interactions in the Karoo, and knowledge gained through modelling should prove to be of economic value to the farming community. I suggested earlier that many lifestyle characteristics of black eagles could be attributed to the relative stability of their prey base. More could be learned about the consequences of the order of magnitude variation in prey bases on raptor lifestyles. With regard to investigations of predator-prey systems which involve refuge, it should be borne in mind that there are likely to be other systems where predators regulate vulnerable prey between limits set by the extent of discrete refuge habitats, but where stochastic change in the degree of protection offered to prey may over-ride statistical detection of any density-dependent responses by the predators.

I have attempted to cover the key elements of this predator-prey system as comprehensively as possible, but more research is still warranted on the following aspects: interactive effects of rainfall, vegetation and herbivory in the lower trophic level; the influence of rainfall on the birth and survival rates of juvenile male and female hyrax; observations of hyrax foraging behaviour during experimental manipulation of predation risk and/or foraging return; comparative morphology and behaviour of rock hyrax inhabiting regions of Africa where black eagles are absent; numbers of hyrax captured by caracals under conditions of normal or high prey availability, and the emphasis of this predation on different hyrax population classes; the involvement of secondary predators in the extensive mortality of juvenile hyrax; and the compensatory behaviour of non-violent hyrax mortality on farms where predators are still controlled. A short-term indication of this compensatory mortality might be gleaned by comparing the bone marrow fat content of fresh hyrax carcasses collected beneath eagle feeding sites with that of hyrax from a randomly shot sample. This might reveal how many hyrax captured by eagles were already likely to die of other causes, but it should be remembered that compensatory non-violent mortality is likely to increase along with hyrax population density in the absence of predators. Other related research fields which would provide useful data would be feeding energetics of captive black eagles on a hyrax diet; post-mortem examinations of fresh lamb carcasses brought to black eagle nests, and an extensive survey by necropsy of factors causing deaths of domestic lambs on karoo farmland. Captive trials on the effectiveness of lithium chloride as a taste-aversion agent to discourage lamb-killing eagles are planned.

*Do black eagles kill domestic livestock in the Karoo, and if so what steps can be taken to prevent this?*

Feeding studies indicate that two black eagle pairs on an average karoo farm in mountainous terrain are likely to consume 6 - 13 domestic lambs annually. Utilisation of this food resource was indicated by earlier nesting by eagles on farmland. It is not known whether such lambs were dead, dying to other causes or healthy when the eagles 'collected' them. But it is probable that 145 lambs die on the average karoo farm annually (mostly just after birth), and that black eagles, like golden eagles, scavenge most of the lambs that they bring to their nests. No reliable conclusions can be drawn from these data but an overall worst-case scenario of 2 - 5 lambs killed annually per farm by black eagles is suggested for mountainous karoo terrain.

Reliable and extensive field necropsy surveys of lamb mortalities under open-range conditions around the world indicate that 20% of lambs born are likely to die before weaning, and that predators are the prime cause of death

University of Pretoria etd – Davies, R A G (1994)



for about 1,7% of lambs born under semi-arid, open-range conditions. Only limited surveys have been conducted in South Africa which indicate lower rates of predation than elsewhere. But black eagles were not implicated in nearly 600 carcass examinations, all of which were conducted in black eagle habitat. Black eagles were exonerated on two out of three carcass inspection surveys conducted on Cape farms in response to farmers complaining of major losses to eagles. It is concluded that lamb-killing by eagles does occur in the karoo but very rarely. Most eagles appear to prefer natural prey, possibly because they became 'wedded' to such prey as nestlings. Being specialist predators of hyrax, black eagles may have a well-developed 'specific search image' for this prey, and unlike other *Aquila* eagles, they are highly territorial and are not recorded to aggregate at lambing paddocks. These reasons are offered to explain why lamb-killing by eagles in mountainous parts of the Karoo occurs less frequently than might otherwise be expected.

Of the 820 lambs born on the average karoo farm each year, 145 are likely to die. Using the very extensive and comparable Australian data (which actually indicated higher predation rates than the South African surveys), it is calculated that (all) predators are likely to be the prime cause of 13,6 of these deaths and eagles are likely to be the prime cause of only 0,32 lamb deaths on the average karoo farm annually. This gives a reliable indication of the overall scale of the problem but some farmers are likely to suffer more losses than others. Problem situations involving eagles can be dealt with by more intensive flock management during the vulnerable lambing period. This can involve the use of shepherds or scarecrows; removal of all carcasses from the lambing area; and conducting lambing away from areas of eagle activity, especially when breeding pairs have young nestlings which may adopt a lamb-eating habit. Taste-aversion using lithium chloride may prove a useful deterrent in the future, but persistent lamb-killers should be trapped and sent to zoos or falconers to prevent further spread of the trait.

*The role of black eagles on karoo farmland*

The net influence of black eagles on human commercial activities in the Karoo can best be judged by comparing the cost of their predation on domestic lambs with the benefits of their predation on rock hyrax, a potential competitor for the veld resource. The current market value of weaned lambs is R74, so the overall cost of lamb predation by black eagles to the average karoo farmer in mountainous terrain, as indicated by extensive and reliable studies of lamb mortality and the relative involvement of predators, is R24. This cost is equivalent to 0,05% of proceeds from lamb sales on the average farm, and would comprise a much smaller equivalent to gross farm income. It is concluded that lamb predation by black eagles in the Karoo is of negligible financial importance overall.

Assessing the financial benefits of black eagles to karoo farmers in terms of alleviation of competition between hyrax and domestic livestock for grazing is more difficult. But an indication of this can be obtained by looking at the increase in numbers that is predicted by the hyrax population model in the absence of predation by eagles. Lensing (1982) has argued that competition between livestock and hyrax on Namibian farms is negligible because livestock rarely venture into the rocky habitats used by hyrax. However, the food requirements of surplus hyrax (defined in the model as the excess of population density over carrying capacity of food supplies within the refuge environment) must be met outside of the vicinity of rocky habitat. On the basis that 10 hyrax consume as much food as an adult Merino

University of Pretoria etd – Davies, R A G (1994)



sheep and current letting rates of R30 per head per year, the additional hyrax surpluses predicted in the absence of eagles (about 622 extra hyrax per eagle territory annually) are likely to cost the average karoo farmer in mountainous terrain (two eagle territories) in the order of R3700 each year. Most farmers control caracals rather than eagles and seldom eradicate either, so impedance of the predation response is a more realistic interpretation, and it is estimated that just a 30% impedance of both caracals and eagles will create additional hyrax surpluses which will consume R2700 worth of grazing annually.

Black eagles are very important members of a guild of predators which are essential for restricting hyrax to their refuge environment and for removing any surpluses. The predicted cost of hyrax surpluses when black eagles are removed from karoo farmland exceeds the estimated overall cost of lamb-killing by black eagles by a factor of 150. Even the cost of the worst-case scenario of five lambs killed by eagles per karoo farm, that is indicated by unreliable prey remains data, is still ten times less than the estimated saving that can be attributed to black eagles through prevention of hyrax surpluses. Eagles would need to kill up to 50 lambs per farm annually before the total removal of eagles would make any financial sense. However, more intensive management of flocks during the crucial lambing period, using practical techniques, should enable karoo farmers to reap the benefits of having black eagles on their farms without incurring any significant costs in terms of lambs lost. The financial benefits of black eagles to karoo farmers greatly outweigh the negligible overall costs, and management can minimise any costs arising in very rare problem situations involving eagles. So I conclude that, in financial terms, black eagles are clearly compatible with the open-range farming of small livestock in the Karoo.

To prevent the development of rifts between farmers and conservationists, it is important that conservation officers do not deny that eagles may kill lambs, and that they take an active interest when farmers report problem situations. From experience gained in the present study, carcass examinations conducted in such 'problem situations' provide real data which usually exonerate eagles and educate both farmer and conservation officer as to the real causes of lamb mortalities, thereby affording ideal opportunities for constructive interaction between two parties who can, otherwise, easily become diametrically-opposed in the absence of reliable information concerning the problem.

Black eagles are evidently extremely efficient at catching rock hyrax so it is likely that they out-compete many other predators for this dominant prey in areas where they are not nest-site limited. Less compatible predators may be attracted by abundant hyrax on farms where eagles have been removed. Caracals are not as obviously compatible with small-stock farming operations as black eagles because certain individuals may cause extensive damage to livestock. But the present investigation indicates that the highly variable capacity of caracals to remove hyrax may have just as much demographic influence in the prevention of hyrax surpluses as specialist predation by black eagles. Where problems occur with caracals it is recommended that farmers adopt the management principles suggested by Stuart (1981a) whereby individuals rather than species are controlled. Gin traps and strychnine are indiscriminate and inhumane methods of control and do untold damage by removing innocent predators, many of which may be important as primary or secondary predators of pest species such as hyrax. These methods should be abandoned forthwith and replaced by toxic collars, cage traps and other selective methods which allow for the effective and humane removal of those individuals responsible for killing livestock.

University of Pretoria etd – Davies, R A G (1994)



Not all the benefits of eagles to farmers can be assessed in financial terms. Eagles are likely to play an important role in preventing the spread of diseases by removing animals whose sickly and aberrant behaviour triggers the predation response. The spread of rabies by small carnivores (e.g. mongooses) may be significantly curtailed by large raptors. This is one way in which eagles act as agents of natural selection and remove unfit individuals, thereby maintaining healthy stock in their prey populations.

It is especially hard to place a value on the aesthetic pleasure that people derive from watching wildlife, especially spectacular and evocative species such as large eagles. Many populations of these large, slow-breeding birds are vulnerable to the effects of people and development, and have declined worldwide. It is likely that with growing human populations in the third world more wilderness areas will lose out to development and eagle populations will decline further through loss of suitable habitat. With the growing popularity of ecotourism, farmers with large eagles on their properties may find that they have a valuable and marketable commodity. A good chance of seeing large eagles is already a 'draw-card' for game lodges and guest houses in South Africa.

But large eagles have probably inhabited southern Africa and the Karoo for 10000 times longer than human beings, and it is a sad view to believe that such wildlife must demonstrate a positive economic value to ensure its survival. Where farmers are still uneducated as to the role played by large eagles in the environment, it may be necessary to stress the financial advantages of conserving such obviously beneficial species as black eagles, as indicated above. But what of species such as martial eagles which do not demonstrate such an easily-identifiable positive role? Progressively more farmers are demonstrating that they certainly do have an aesthetic appreciation of, and enjoy, the wildlife on their farms. In some areas this has almost grown into a competition among peers to boast such flagship species as eagles on their land. I suggest that future education campaigns pay progressively more attention to instilling this aesthetic appreciation of wildlife among landowners and encouraging the conservation of species which do not necessarily demonstrate a noticeable positive role, rather than simply stressing the financial advantages of mutually-beneficial species.

Many of the current ecological problems in the Karoo, such as degradation of the vegetation resource and irruptions of pest species, can be associated with simplification of this ecosystem by human activities. By replacing the diverse plains game with monocultures of livestock, and by eradicating many carnivores, scavengers and even beneficial insectivores, some key players in a once-diverse system have been taken out. With its stochastic, water-limited climate the Karoo could not have been described as truly stable before the advent of farming, but these arid systems are especially sensitive to interference, and simplification tends to reduce the stability of ecosystems. Just tolerance of compatible predators such as large eagles is one simple and easy management step that karoo farmers can take to restore the ecology on their farm to something of its former diversity and stability.

University of Pretoria etd – Davies, R A G (1994)



## SUMMARY

Grazing resources in the Karoo and in Namibia have been damaged in the past by 'irruptions' of rock hyrax which have been attributed by some naturalists to predator eradication. But many ecologists have maintained that predators do not limit or regulate their prey in vertebrate communities. The highly specific predator-prey relationship between black eagles and rock hyrax is ideally suited to an investigation of predation. A study of this system was initiated to assess the impact of black eagles on their prey (including domestic livestock) in terms of numbers and population dynamics, and so resolve the predation debate with regard to this system and establish the role of this predator on karoo farmland. The study also afforded the opportunity of investigating how the 'lifestyles' of black eagles and rock hyrax have become inter-linked. Certain key elements were identified in this predator-prey system including an important alternate prey species and an important competing predator species. During a five year field study, all elements were researched as comprehensively as possible to construct 'as good a model as possible' of the system which is used in conjunction with the results of the field study to address key questions regarding the demographic influence of black eagles on rock hyrax.

The study was conducted in the semi-arid interior of the Cape Province known as the Karoo, an extensive dwarf shrubland which is prone to a stochastic climate and droughts, but which supports an important small livestock industry. Livestock predation by black eagles was investigated on farmland throughout the central Karoo, but the Karoo National Park (KRNP) at Beaufort West was chosen for the detailed study of the demographic influence of black eagles on rock hyrax. This site was representative of mountainous regions in the Karoo and contained natural populations of predators which had not been persecuted for seven years prior to the present study. Rocky habitats in the park comprised prime habitat for both rock hyrax and black eagles and there was no indication that the eagles were limited by nest sites. The summer rainfall regime experienced in the Karoo is somewhat cyclic: excellent rains in the late 1970's were followed by major drought in the early 1980's, and previous researchers in the KRNP recorded a fourfold decline in hyrax prior to the present study. Rainfall during the study period was average, so this could be regarded as a period of recovery for karoo biota.

It was established early on in the study that refuge played a key role in this predator-prey system. All rock outcrops (n=3365) in the central part of the park (140km$^2$ - encompassing more than four eagle territories) were classified and described in detail, and then mapped onto a geographical information system (GIS) of the study area to allow detailed measurements. Mudstones form the bulk of karoo bedrock but are not sufficiently resistant to form outcrops. The characteristic koppies and plateaus of the Karoo are created by resistant sandstone lenses and intrusions of dolerite. Two major dolerite sills are exposed as an upper and lower escarpment in the KRNP, and divide the park into five major topographical habitats: upper plateau, upper slopes, middle plateau, lower slopes and bottom plains. Continuous lineal outcrops (dolerite escarpment and lineal sandstone outcrops on slopes) occupied 3% of the mapped area. Discontinuous screes and dolerite knolls were scattered over a further 14% of the area. Most rock outcrops were exposed on the mountain slopes (84% of lineal outcrops, 98% of screes). Highest densities of apparently suitable crevices (for hyrax) were recorded in lineal sandstone outcrops and where dolerite escarpment had weathered into pillars.

The rock hyrax prey base in the KRNP was studied by annual intensive counts at colony outcrops and by plotting all hyrax groups within the mapped area. Population estimates (end 1989) were 1025 for an average eagle territory and 13335 for the park. Density (69 per km$^2$ in mountainous terrain) was much lower than recorded elsewhere. Over 98% of hyrax in the KRNP occurred in groups and all overnighted in rock outcrops which had been rated at least adequate for colonies (none in temporary shelter). Larger groups occurred closer together in the large, crevice-rich igneous escarpment outcrops, especially where these converged into kloofs with boulder screes and dense vegetation. Groups were often located close to riparian thicket. The distribution suggested that 'safely-accessible food' was most important, and that within group ranges suitable overnight shelter was not limiting. Most groups occurred on slopes (where most rocks were) and there was some

University of Pretoria etd – Davies, R A G (1994)



favouring of east-facing aspects which receive early-morning sun. Despite these trends groups were fairly regularly distributed through adequate habitat. Despite some habitat-related variation, most harem groups approached an average of 16,4 members. Disappearance/coalescence of small groups and the tolerance of sexually-quiescent males within harems suggested that maintenance of adequate group size was important. Predation risk is considered the main reason why hyrax spent 96% of their time within 5m of shelter and never ventured further than 15m from a bolt hole. Distinct vegetation zones around well-used outcrops conformed to this pattern. Hyrax posted sentinels and used screes and thickets to access quality vegetation on intense group-feeding bouts and made extremely efficient use of this time away from their shelters by harvesting different parts of their range on consecutive days. These trips were not made on windy days. Dispersal through non-rocky terrain occurred at night. Predation pressure may also explain why hyrax in the unpredictable Karoo show a distinct birth-pulse (modal parturition date 12 Nov). Composition of the hyrax population was determined from the three age classes recognisable during counts immediately after the birth-pulse, and from life-table analyses of skulls collected in the field. Variable mortality and especially recruitment rates related to rainfall and caused a significant population decline in the dry year of 1988. There were indications of late pre-natal mortality in very dry conditions, and that sex ratio of the first age class varied with rainfall. Hyrax population structure is evidently highly dynamic in response to the stochastic rainfall of the Karoo.

Transect sampling of the major habitats in the KRNP revealed that middens of Smith's red rock rabbits occurred at densities of 400 - 500 $km^{-2}$ in mountainous terrain. Studies of faecal accumulation rate on middens indicated a ratio of one animal to about 15 middens. An overall density of 30 rabbits $km^{-2}$ was inferred with an estimate of 6652 for the KRNP in 1989, and 441 for the average (lower escarpment) eagle territory. But incidental sightings of rabbits suggested a ten-fold increase in numbers by 1989 from a 'low' in 1987. Other potential prey populations also showed 'troughs' in numbers in 1987 or 1988 which were probably drought-related. Red rock rabbits did not occur on the non-rocky bottom plains, but were relatively homogeneously distributed through the mountainous habitats - so they occurred at one third the density of rock hyrax on mountain slopes, but double their density on the rocky plateaus. Some variation in midden density indicated that loose rocks strewn over gentle slopes were preferred, while grassy, northerly aspects were avoided (possibly for thermoregulatory reasons). Sitings of middens indicated that some access to rock crevices is a prerequisite for the ranges of individual rabbits - these may serve as bolt-holes for adults or nest sites for young. Defence of these discrete, limited resources is offered as an explanation for territorial behaviour in this species.

Twenty two pairs of black eagles were located in the study area (13 nested in the park). This density (4,14 pairs per 100$km^2$) is higher than all estimates from other mountain ranges except the Matobo Hills. Eagle pairs nested significantly closer together along the upper escarpment (mean 2,7km) than along the lower escarpment (mean 4,6km), and the former represents the closest nest-spacing yet recorded for any linear mountain feature. Floaters (> 40% immatures) probably occurred at a ratio of one per 15 resident pairs. The continental escarpment ranges in the Karoo are likely to accommodate over 600 pairs, and the entire mountain ranges in the Cape over 2000 pairs. The habits of black eagles preserve them from most forms of human persecution which have eradicated large scavenging raptors from the Karoo. Black eagle pairs in the KRNP occupied inter-locking territories with no unused space. Overlap between pairs was minimal (<10%) especially for foraging behaviour. Average territory size was 24$km^2$. Three pairs each defended 52km of lineal rock outcrops, a fourth 60km. But the safe feeding area for hyrax around rock outcrops was the habitat parameter which showed least variation across territories. An hypothesis that eagles might use rocky habitats as a structural cue for stable territories despite fluctuating hyrax numbers is not supported by recent observations of territory vacation in the Matobo Hills. Territories also contained relatively consistent amounts of food (mean 63 hyrax groups) and an abundance of prey refuge (mean > 44000 crevices). Nearly all nests were located in core areas of territories, but radio-carbon dating of material from one tall nest (3,8m) did not supply evidence that nests (and thus perhaps the core areas) were very ancient. Nests were preferentially sited on tall sheer dolerite cliffs facing south. Relatively late breeding (except on farmland) and small clutch size were suggestive

University of Pretoria etd – Davies, R A G (1994)



of low food availability, but overall breeding effort (61% pairs) and success (46% pairs) was not dissimilar to that recorded elsewhere. Most nest failure occurred on accessible lower escarpment cliffs at the small chick stage, and could be attributed to predation by mongooses twice. Pairs suffering high failure rate tended to have more alternate nest sites. Large lower escarpment territories probably contained more prey for despite high failure rate, these pairs made more breeding effort and raised more chicks than upper escarpment pairs.

Black eagles spent 24% of their daytime flying, and allocated slightly more of this flying time to territorial defence than to foraging. Eagle flight paths recorded during 40d of watching resident pairs were analysed by GIS. An average flight speed of 47kph (range 10-125kph) was calculated from 693 flights covering 2747km and spanning 58h. The timing of hunting flights and strikes at prey showed seasonal change which matched the changing foraging rhythms of hyrax. Eagle foraging behaviour was state-dependent and weather-dependent. Eagles flew more on windy days. Hunting eagles flew mostly over slopes which were close to their nests, afforded good hyrax habitat and good lift for prevailing wind sources. They preferred to first sight their prey from a perch or high altitude flight and then make a hidden approach. Only 8% of strikes at prey resulted in kills. Strikes from perches were twice as successful as strikes from flights, and tandem strikes were twice as successful as solo strikes, but these improvements were not statistically significant. Eagle pairs spent 85% of their flight time together. When hunting in pairs, black eagles fulfilled most of the characteristics of cooperative hunting, and their division of labour could usually be related to the dimorphic capabilities of the sexes.

Radio-tracking of four caracals in the KRNP was unsuccessful, but trapping success experienced during the capture of these animals suggested intermediate density (4,8 adult units per 24km$^2$ eagle territory) between that recorded in the south-west Cape (2,4 adult units per 24km$^2$) and that recorded in the eastern Karoo (7,4 adult units per 24km$^2$), and this would concur with intermediate rainfall. Caracals are likely to outnumber black eagles by a factor of three in the KRNP, and metabolic predictions suggest that they might consume nearly six times as much food. Unlike black eagles, the flexible social organisation of caracals allows them to show a significant numeric response to changes in prey availability. The density estimates from elsewhere in the Cape provide likely upper and lower limits to this response. Long-term trapping records of caracals on farms suggest that numbers may increase by up to 22% p.a., and decrease by up to 34% p.a. in conjunction with major rainfall events (after a time-lag of 6-12 months). Hyrax can comprise over 50% of caracal food in the Karoo, but no hyrax remains were found in 100 caracal scats analysed in the present study. As generalist predators, caracals were relying on other prey, notably wild and domestic bovids. Secondary predators occur in sufficient numbers in the KRNP (@ six per 24km$^2$) to pose a significant additional threat to juvenile hyrax.

Feeding trials and metabolic predictions indicated that an average black eagle needs to consume between 1500 and 1700 KJd$^{-1}$ food energy for maintenance in captivity. Approximately 500g of hyrax would fulfil this requirement allowing for 40% wasted and 75% metabolised. It is likely that wild nestlings can get by on slightly less food than this (overall), but that wild adults may need up to 25% more. Field observations and time-lapse photography at nests indicated that eagle pairs were catching 0,43 prey/d when not breeding and 0,57 prey/d when provisioning young. Eagles had to catch an additional prey item every five to six days when provisioning young but this requirement varied with nestling age. These prey capture rates were much lower than those recorded in similar studies of black and other large eagles. But mean prey mass was much larger (2565g) such that rates of biomass captured (446kg/y) and consumed (284kg/y) by breeding pairs were not markedly dissimilar from other studies. Observed rates of food consumption were still lower than the predicted minimum requirements (especially when breeding), and eagle pairs with a large lagomorph component in their diet were able to achieve higher provisioning rates, so low hyrax availability is inferred. Prey capture rate did not vary with nestling food requirement nor the hunting abilities of the pair. High rates of hyrax deliveries to nests coincided with periods of drought and with the time of day when hyrax were likely to be foraging.

University of Pretoria etd – Davies, R A G (1994)



Rock hyrax comprised 88% of 3823 prey items identified from remains collected beneath black eagle eyries in the study area. In comparison with other studies of black eagle diet by the same method, this is average to high and does comply with the popular belief that black eagles are highly prey-specific. However, comparison with time-lapse photography and other methods indicated that rock hyrax remains are significantly over-represented in collections of prey remains, and small lagomorphs are extremely under-represented. The most likely composition of black eagle diet was interpolated from various methods: hyrax comprised 67% (range 46-83% for different pairs from reliable data), lagomorphs 25%, bovids 4% and carnivores 2% by frequency. Most prey items (97%) fell in the size range 500-4000g. Juveniles predominated among bovid prey, and eagles generally avoided this category presumably because of risk of injury. Domestic lambs comprised 1,2% of prey remains, and up to 3,4% of prey deliveries to nests on farmland. It is not known how many of these were scavenged, but carrion might fulfil 4-11% of eagle food needs. Upper escarpment eagle pairs, despite smaller territories, took more alternate prey (especially birds and reptiles) than lower escarpment pairs. The composition of prey in black eagle diet was very similar to the composition of prey available (except for avoidance of bovids), so are black eagles truly prey-specific? Many lines of evidence indicated that hyrax were well-protected within their refuge environment during the field study, and this low availability was reflected in the absence or low frequency of hyrax in the diet of two large generalist predators in the area. Also, there was no evidence of a switch response in black eagle diet to increased abundance of red rock rabbits. It is concluded that black eagles were behaving as specialist predators by pursuing their favoured prey despite low availability.

The age and sex of hyrax maxillae belonging to 3359 hyrax eaten by black eagles in the KRNP and 2259 hyrax eaten by black eagles elsewhere in the Cape were determined from patterns of tooth eruption and tooth wear. Composition of population classes among KRNP prey were compared with composition of the prey population. Eagles showed avoidance for the very abundant first age class, presumably because juveniles are of low profitability (1/16 of adult mass at birth). Eagles showed positive preference for immature hyrax (1-2y olds) which comprised the most frequent age class captured. Eagles caught significantly more immature males than females, and this heavy predation was partly responsible for the observed skew in the adult prey population towards females. Dispersal is more obligatory for immature males, and these animals presumably become more vulnerable to eagle attack when they enter unfamiliar terrain without the advantages of group vigilance and sentinels. Adult hyrax are presumably more experienced at evading eagles and did not occur more frequently among eagle prey than expected. But eagles exerted hard selection on adult and old hyrax, and could account for three out of every four deaths among these age classes. Old hyrax (8-13y) fell prey to eagles more frequently than expected, presumably because of deteriorating flight response, and the eagles were able to remove one third of these hyrax annually. More old female hyrax were available to the eagles than old males, but they were still captured significantly more frequently than expected. This may be because females are more inclined to adopt high-risk sentinel behaviour, and other factors may be more involved in the deaths of males. So the overall pattern of age-selective predation of hyrax by black eagles could be explained in terms of vulnerability rather than 'prudent predation'. This pattern showed great geographical and temporal variation which correlated significantly with respective rainfall patterns prior to the collections - testament to the dynamic nature of hyrax population structure and to the validity of the methods used for age-determination. The size of adult hyrax captured (as indicated by maxillae) also correlated with rainfall patterns. Lower escarpment eagles preyed more heavily on surplus elements in their hyrax prey base, such as males and old hyrax. Upper escarpment eagles captured relatively more unprofitable juveniles and healthy breeding stock such as adult females (along with more alternate prey). Upper escarpment eagles were thought to be suffering low hyrax:eagle ratios, and this was also suggested by reduced wastage (more hyrax crania opened). These symptoms of low hyrax:eagle ratio were also evident in eagle diet from low hyrax density mountain ranges (e.g. Fynbos), and in eagle diet when hyrax were at low abundance and reduced availability (E. Cape & Fynbos during early 1970's).

Early nesting by black eagles on farmland suggested that these pairs were utilising food resources unavailable in the KRNP. Nest-based studies of feeding habits indicated that black eagles were consuming 6-13 domestic lambs annually on the average karoo farm in mountainous terrain (= two eagle territories). These studies did not indicate whether these lambs were

University of Pretoria etd – Davies, R A G (1994)


healthy, dying or dead when 'collected' by the eagles. About 20% of lambs die before weaning, which would leave about 145 carcasses available to eagles per karoo farm. It seems likely that black eagles, like golden eagles, scavenge most of the lambs brought to nests. Surveys of lamb mortality by field necropsy in lambing areas yield the most reliable and comprehensive indication of livestock predation. Extensive surveys of Merino mortalities under open-range conditions in Australia (very comparable to the Karoo) indicate that predators are the prime cause of death for 1,7% of lambs born, and worldwide surveys indicate that eagles may be responsible for 2,4% of predator kills. Limited mortality surveys in South Africa (in black eagle habitat) indicate lower losses to predators and no involvement of eagles. In the absence of good karoo data, the Australian data indicate that the overall cost of livestock predation by eagles to karoo farmers is likely to be 0,32 lambs or R24 - i.e. negligible. Direct observations suggested that most eagles in the Karoo prefer natural prey, to which they may have become 'wedded' as nestlings. Unlike other large eagles, black and martial eagles are not recorded to congregate in lambing areas. Nevertheless there is proof that black eagles have killed lambs in the Karoo and it is likely that such problems would be concentrated on a minority of farms. It is suggested that affected farmers manage their flocks more intensively during lambing by the use of shepherds/scarecrows, by removal of carcasses and by conducting lambing away from areas of eagle activity. Flock management is far more effective than predator management (e.g. eagle translocation), but taste-aversion may prove useful in the future, and persistent offenders should be removed (to zoos/falconers) to prevent spread of a lamb-killing trait.

Rock hyrax were at low density and low availability during the present field study. During the years of accurate data collection, black eagles removed an average of 11% (117) of the hyrax standing crop (1062) per territory per annum. They also removed 8% of the red rock rabbit standing crop (11% in 1989). The hyrax toll taken by the eagles could account for 27% of hyrax mortality and was equivalent to 29% of annual hyrax recruitment. Key-factor analysis indicated that hyrax population change during the study period was more related to losses through the upper trophic level (predators) than to losses through the lower trophic level (loss of breeding potential and non-violent mortality). The study was presumably too short to confirm any density-dependence of demographic factors, but mortality was more closely related to density than recruitment. Presumably reproduction would only be hampered by crowding effects at high density. Despite changes in hyrax density, eagles consistently removed 11% of the population. Many hyrax killed by eagles were from age classes with high survivorship, so it is likely that much of this mortality was additive, and therefore it can be stated that the eagles exerted a limiting influence on hyrax population growth during the field study. Fluctuating food supplies and a hyrax population with high propensity for increase is a potentially unstable situation - any factor which acts as a consistent 'handbrake' on population growth should help prevent imbalances developing between the population and food supplies.

Data from the present study and other field research were collated to develop a detailed and specific hyrax population model which simulated hyrax demography in response to long-term climatic data for the Karoo. The model departs from previous hyrax modelling attempts in precise measurement of the refuge environment and its carrying capacity (set by food), and by allowing this carrying capacity to vary in a simple lower trophic sub-routine which accommodated herbivory and the profound effects of rainfall (enrichment). Population processes are dependent in the model on the ratio of the hyrax population (P) to this dynamic carrying capacity (K), such that small hyrax populations after good rains experienced minimum mortality and maximum recruitment, whilst large populations during drought experienced the opposite. The model shows that natural predation enables hyrax populations to closely track climate-induced changes in their food supplies within the confines of their refuge environment. Irruptions of hyrax reported in the literature corresponded to predicted decline phases - these hyrax probably became more noticeable because of habitat shift and dispersal in response to pasture exhaustion within the refuge environment. The puzzling widespread decline of hyrax in the early 1980's can be explained in simple terms of enrichment followed by severe drought. Predictions of this decline for different rainfall regimes showed strong correlations with field observations of hyrax in the KRNP and black eagles in the Matobo Hills. Climate-induced irruptions are more likely to occur in arid regions with stochastic rainfall. So irruptions were primarily caused by pasture exhaustion, but predator eradication

University of Pretoria etd – Davies, R A G (1994)



is likely to have greatly aggravated the irruption reported in the 1940's. Key factor analyses and simulated removal or impedance of predators demonstrated that the variable predation response had the capacity to remove hyrax surpluses as they arose (even at high density). Although modelled on P:K ratio, variable recruitment and non-violent mortality in the absence or impedance of natural predation were insufficient to prevent rapid departure of P from K which resulted in large hyrax surpluses and regular population crashes when heavy compensatory mortality was predicted due to grave imbalance with food resources. These predictions were robust for a wide range of dramatic parameter perturbations. Annual variation in the number of protected hyrax obscured density-dependence in the predation response, but it can be stated that predators still regulate hyrax populations in the lenient sense of the term by confining them to refuge patches and by ensuring persistent fluctuation within limits set by minimum and maximum food supplies within the refuge patches. Pasture exhaustion during severe drought may occasionally force large surpluses of hyrax from their refuge patches but the natural complement of predators has the capacity to remove these animals. Separate impedance of black eagles and caracals in the model did not indicate any obvious difference in the demographic influence of these very different predators, but it was clear that the full complement of predation was required for regulating the hyrax population and this was confirmed by field indications of hyrax population change on a farm where all predators except black eagles were persecuted. Hyrax populations differ from cyclic prey populations because increase and decline phases are irregular and climate-induced, but unlike the environmentally-modulated predator-prey systems described in Australia, hyrax populations do not naturally escape the local predation capacity. The unique character of the black eagle - rock hyrax system can be attributed to the influence of a permanent and highly effective refuge habitat, and to the destabilising phenomenon of reduced prey availability despite increasing abundance during enrichment.

Black eagles were reliant on rock hyrax as their principal food in this and other studies in Africa, and exerted very hard selection on adult and old hyrax, so it was not surprising that a comparison of the functional morphology and ethology of rock hyrax and black eagles revealed traits that appeared to have evolved reciprocally between the species. Both show obvious adaptations to their habitat as well as to each other, and such adaptations have probably reinforced their mountain lifestyles. To avoid predation, hyrax minimised their time away from shelter (especially on windy days when eagles were more active) and made use of an early-warning system when foraging in groups. In response: eagles timed their hunts to coincide with hyrax foraging rhythms; they hunted cooperatively to allow double strikes at elusive prey and to capture prey which took refuge in vegetation; and they made maximum use of cover and adverse light conditions to conceal attacks. A special light-shielding structure has evolved in the eyes of rock hyrax which may facilitate detection of attacking eagles, while disproportionately large feet are likely to be an adaptation of black eagles for capturing hyrax which are twice as large as normal *Aquila* prey. Many aspects of black eagle lifestyle, such as their striking territorial behaviour and their conservative reproductive behaviour, can be linked to the unusual degree of stability of the hyrax prey base which can be attributed to the permanent and patchy distribution of a very effective refuge resource.

Black eagles have been known to kill domestic lambs, but it happens so rarely that the overall cost to karoo farmers is negligible. When farmers complain of problems with eagles, these situations can be investigated by examining carcasses in the lambing areas to reveal real causes of lamb mortality - this approach is far more constructive than denial of the problem which can often lead to rifts between farmers and conservationists. If eagles are implicated then management practices can be recommended which should minimise or prevent losses. But it is likely that the examinations will exonerate eagles of blame, and they will have afforded an opportunity for education. The present study indicates that financial benefits of black eagles on farmland, in terms of grazing saved from hyrax surpluses, may outweigh overall costs by a factor of 150. Financial advantages of conserving such obviously beneficial species can be stressed in education campaigns, but these campaigns should not neglect species which have less obvious financial or ecological benefits. Tolerance of compatible predators such as large eagles is one simple and easy step that karoo farmers can take to restore the ecology on karoo farmland to something of its former diversity and stability.

University of Pretoria etd – Davies, R A G (1994)



# OPSOMMING

Weiding in die Karoo en Namibië is in die verlede beskadig deur "uitbrake" van klipdassies wat, volgens sommige natuurkenners, deur die uitroei van roofdiere veroorsaak is. Daarenteen is baie ekoloë van mening dat, binne vertebraat-gemeenskappe, roofdiere nie hul prooigetalle beheer nie. Die spesifieke roofdier-prooi verhouding tussen dassies en witkruisarende is 'n ideale onderwerp vir so 'n studie. So 'n ondersoek is onderneem met die oog daarop om die invloed van arende op hul prooi (insluitende vee) se getalle en bevolkingstruktuur te bepaal. Op hierdie wyse kan die reguleringsvraagstuk vir hierdie stelsel opgelos word, en die rol van arende binne die Karoo-omgewing te bepaal word. Die studie bied ook die geleentheid om te bepaal hoe die biologie van die roofdier en prooi wedersyds beïnvloed word. Alternatiewe prooi vir die arende en addisionele predasie deur ander roofdiere blyk belangrike fasette van die stelsel te wees. Die resultate van vyf jaar se veldwerk, waartydens alle aspekte van die stelsel so intensief moontlik ondersoek is, word gebruik om 'n model saam te stel wat die belangrike vrae rakende die invloed van witkruisarende op die demografie van dassies aanspreek.

Die studie is gedoen in die half-droeë Karoo van die sentrale Kaapprovinsie, 'n uitgebreide bossieveld wat aan 'n wisselende klimaat en aan droogtes onderhewig is, maar wat 'n belangrike kleinveebedryf huisves. Predasie van arende op kleinvee is ondersoek op plase dwarsdeur die sentrale Karoo, maar 'n diepgaande studie van die demografiese invloed van arende op dassiebevolkings is in die Karoo Nasionale park (KRNP) te Beaufort-Wes onderneem. Hierdie nasionale park verteenwoordigend die bergagtige Karoo wat beskik oor natuurlike bevolkings roofdiere wat gedurende die voorafgaande sewe jaar nie gejag is nie. Klipperige habitat het goeie woonplek verskaf aan beide dassies en arende en daar was geen aanduiding dat die getal arende beperk is deur 'n gebrek aan nesmaakplek nie. Die somer-reënval in die gebied is deels siklies: hoë reënval gedurende die laat 1970's is gevolg deur ernstige droogtes gedurende die vroeë 1980's. Vorige navorsing het getoon dat dassiegetalle in die KRNP viervoudig verminder het gedurende hierdie tydperk. Vir die duur van die studie was die reënval gemiddeld gewees en gedurende hierdie tydperk het die Karoo se diere- en plantelewe waarskynlik herstel van die droogte.

Dit het gou duidelik geword dat skuiling 'n sleutelrol in die roofdier-prooistelsel inneem. Alle klipkoppies (n=3365) in die sentrale deel van die KRNP (140 $km^2$ - wat meer as vier arend-territoria insluit), is in besonderhede beskryf en geklassifiseer. Die klipkoppies is deur middel van 'n geografiese inligtingstelsel (GIS) gekarteer sodat noukeurige metings gedoen kon word. Sedimentêre gesteentes vorm die grootste deel van die Karoo se grondlaag, maar is nie hard genoeg om klipkoppies te vorm nie. Die kenmerkende koppies van die Karoo word deur formasies van sandsteen en doleriet gevorm. Twee groot doleriet-vlakke vorm 'n hoë en lae platorant in die KRNP, en veroorsaak dat die park in vyf topografiese habitatte verdeel kan word: boonste plato, hoë hellings, middel-plato, lae hellings en vlakte. Aaneenlopende, liniêre koppies, bestaande uit doleriet dagsome en sandsteen koppies op hellings, beslaan 3% van die gekarteerde oppervlak. 'n Verdere 14% van die oppervlak word beslaan deur verspreide bergpuin en dolerietbultjies. Die meeste klipkoppies is teen die berghellings geleë (84% van die liniêre koppies, 98% van die bergpuin). Die hoogste digtheid van geskikte skeure vir dassies is in liniêre sandsteenkoppies gevind, sowel as in die verweerde rotspilare van die doleriet-platorand.

Die dassie-prooibevolking in die KRNP is jaarliks intensief by hul koppies getel en gekarteer. Bevolkingskattings (einde 1989) was 1025 vir 'n gemiddelde arend-territorium en 13335 vir die hele park. Die dassie-digtheid (69 $km^{-2}$ in bergagtige gebied) was baie laer as wat blyk uit opnames wat elders gedoen is. Meer as 98% van die dassies in die park het in groepe voorgekom en almal het oornag in klipkoppies wat geklassifiseer is as permanente dassie-skuilplek. Groter groepe is in die skeur-ryke stollingsgesteentes van die platorant gevind, veral in die omgewing van klowe met bergpuin en digte bos. Dassiegroepe is dikwels naby bos langs spruite gevind. Hul verspreiding het aangetoon dat voedsel naby toeganklike skuiling, 'n beperkende faktor is maar dat skuiling waarin oornag word, nie 'n beperkende faktor is nie. Die meeste groepe het teen glooiings voorgekom (waar die meeste klipskuiling was). Daar was tekens van 'n voorkeur vir oos-liggende hellings

University of Pretoria etd – Davies, R A G (1994)



waarop die oggendson skyn. Afgesien hiervan is groepe redelik eweredig versprei in geskikte habitat. Die haremgroepe het 'n gemiddelde grootte van 16,4 dassies gehad, met habitat-afhanklike variasie. Die verdwyning of samesmelting van klein groepies en die verdraagsaamheid teenoor nie-telende mannetjies binne haremgroepe het getoon dat die instandhouding van 'n voldoende groepgrootte belangrik was. Predasie word beskou as die hoofoorsaak daarvoor dat dassies 96% van hul tyd binne 5 m van skuiling bestee en nooit verder as 15 m daarvandaan wegbeweeg nie. Hierdie gedrag is bevestig deur kenmerkende plantegroei-sones rondom goedbewoonde koppies. Dassies het 'brandwagte' en gebruik bergpuin en digte bos om by hoë-gehalte voedsel uit te kom gedurende intense groepvoedingsaktiwiteit. Hulle maak van verskillende dele van hul woongebied gebruik gedurende opeenvolgende dae. Gedurende winderige dae het sulke gedrag nie voorgekom nie. Verstrooiing oor nie-klipperige habitat het snags plaasgevind. Predasie mag ook die oorsaak wees dat dassies in die onvoorspelbare Karoo 'n duidelike geboorte-puls, toon (modus 12 Nov.). Die samestelling van die dassiebevolking is bepaal deur tellings van drie waarneembare ouderdomsklasse onmiddelik na die geboorte-puls sowel as deur die saamstel van lewenstabelle van skedels wat in die veld gevind is. Variasie in geboortes en sterftes het verband gehou met reënval. Dit het veroorsaak dat 'n betekenisvolle afname in getalle plaasgevind het gedurende die droë 1988. Daar was aanduidings dat voorgeboortelike sterftes gedurende droë toestande plaasgevind het en dat die geslagsverhouding van pasgebore dassies deur reënval beinvloed is. Die dassie-bevolkingstruktuur is hoogs veranderlik weens die onvoorspelbare reënval van die Karoo.

Transek-monstering van die belangrike habitatte in die park het getoon dat mishopies van Smith se klipkonyne voorgekom het teen 400-500 km$^{-2}$ in die bergagtige gebied. Die ophoping van mishope het aangetoon dat een konyn ongeveer 15 mishopies veroorsaak. 'n Digtheid van 30 konyne km$^{-2}$ is hieruit afgelei, met 'n skatting van 6652 vir die park gedurende 1989 en 441 konyne in 'n gemiddelde arend-territorium langs die lae platorand. Onbeplande waarnemings het egter gedui op 'n tienvoudige toename in die aantal konyne vanaf 1987 to 1989. Ander potensiële prooispesies het gedurende 1987 en 1988 bevolkingslaagtepunte getoon, waarskynlik weens die droogte. Klipkonyne het nie op die nie-klipperige vlaktes voorgekom nie, maar was relatief eweredig versprei langs die bergagtige habitat - teen 'n derde van die dassie-digtheid teen die hellings maar teen dubbeld die dassie-digtheid op die plato-gebiede. Variasie in die digtheid van konynmishopies het getoon dat gebiede met los rotse langs vlak hellings verkies word, terwyl grasserige, noordliggende glooiings vermy is, moontlik weens effekte t.o.v. termoregulering. Die plasing van mishopies het aangedui dat toegang tot rotsskeure 'n vereiste is vir individuele konyne - moontlik as skuiling of as teelplekke. Die territoriale gedrag van die konyne kan moontlik verklaar word deur die verdediging van hierdie verspreide, beperkte hulpbronne.

Twee-en-twintig pare witkruis-arende het die studiegebied bewoon, waarvan 13 binne die park gebroei het. Uitgesonder vir die Matobo heuwels is hierdie digtheid (4,14 pare km$^{-2}$) hoër as vir enige ander berggebiede. Arendpare het nader aan mekaar nesgemaak teen die hoë platorand (2,7 km; die hoogste witkruis-arend digtheid in enige liniêre bergreeks) as teen die lae platorand (4,6 km). Rondswerwende arende (>40% onvolwassenes) kom waarkynlik voor teen 'n verhouding van een dier per vyftien broeipare. Die kontinentale platorand van die Karoo huisves waarskynlik meer as 600 pare, en die berge van die Kaapprovinsie meer as 2000 pare. Witkruisarende se gewoontes beskerm hulle teen die vorms van menslike vervolging waaraan ander aasvretende roofvoels in die Karoo blootgestel is. Territoria van witkruisarende in die park was gemiddeld 24 km$^2$ groot, het nie oorvleuel nie en het ook geen onbenutte oppervlak gelaat nie. Oorvleueling tussen territoria was minimaal (<10%), veral tydens jag-gedrag. Drie pare het 52 km platorand verdedig en 'n vierde paar het 60 km verdedig. Die hipotese dat arende die teenwoordigheid van klipkoppies, en nie dassie-digtheid nie, gebruik as maatstaf vir territoriumgrootte, is strydig met onlangse waarnemings in die Matobo heuwels waar arende hul territoria verlaat het. Territoria in die KRNP het relatiewe konstante getalle dassies (gemiddeld 63 dassie groepe) en prooi-skuiling (>44000 klipskeure) bevat. Amper alle neste was binne die kerngebiede van territoria, maar radiokoolstofbepalings van 'n 3,8m-hoë nes het getoon dat die neste en moontlik kerngebiede nie baie oud is nie. Neste is meesal gebou op hoë, suidliggende kranse. Laat broeigedrag (behalwe op plase) en klein broeisels hou moontlik verband met lae voedselbeskikbaarheid. Die algehele

University of Pretoria etd – Davies, R A G (1994)



broeitempo (61% pare) en broeisukses (46% pare) het egter nie verskil van dié vir arende in ander gebiede nie. Broeimislukkings het hoofsaaklik in die vroeë kuikenstadium op toeganklike kranse op die lae platorand plaasgevind. By twee geleenthede is dit aan predasie deur muishonde toegeskryf. Arende wat baie broeimislukkings gehad het, het meer neste gehad. Groot territoria langs die lae platorand het meer dassies bevat en het, ondanks 'n laer broeisukses, meer broeipogings en meer kuikens gelewer.

Arende het bedags 24% van die tyd gevlieg. Daar is effens meer tyd aan territoriale verdediging bestee as aan jag. Die vlugroetes van broeipare vir 40 waarnemingsdae is d.m.v. 'n GIS gekarteer. 'n Gemiddelde vlugspoed van 47 $kmh^{-1}$ (10-125 $kmh^{-1}$) is bereken uit 693 vlugte wat 2747 km en 58 h beslaan. Die voorkoms van jagvlugte en aanvalle het seisoenaal gewissel en het saamgeval met veranderinge in die voedingsaktiwiteit van dassies. Jag deur arende was toestand- en weerafhanklik. Arende het meer gedurende winderige dae gevlieg en het geneig om naby hul neste te vlieg oor hellings wat goeie dassie-habitat en gunstige lugstrome gehad het. Hulle het geneig om hul prooi eers van 'n hoë sitplek of vanuit 'n hoë vlug waar te neem en om dan 'n verskuilde aanval te loods. Slegs 8% van die aanvalle was suksesvol. Aanvalle vanaf sitplekke was tweemaal so suksesvol as die vanuit 'n vlug, en aanvalle deur 'n paar was tweemaal so suksesvol as die deur 'n enkele arend. Hierdie verskille was egter nie statisties betekenisvol nie. Arend-pare het 85% van hul vlugtyd saam gevlieg. Terwyl hulle in pare gejag het, is die meeste van die kenmerke van ko-operatiewe jag waargeneem. Hul werksverdeling het gewoonlik met die dimorfisme tussen geslagte verband gehou.

Radio-opsporing van vier rooikatte in die KRNP was onsuksesvol. Uit die sukses tydens die vangs van hierdie roofdiere het dit geblyk dat hulle teen 'n gemiddelde digtheid voorkom, wat waarskynlik verband hou met die gemiddelde reënval van die KRNP vergeleke met ander plekke waar rooikatte bestudeer is (suid-wes Kaap: 2,4 volwassenes per 24 $km^2$; oostelike Karoo: 7,4 volwassenes per 24 $km^2$). Binne die park is rooikatte waarskynlik drie maal so volop as witkruisarende, terwyl voorspellings met betrekking tot metaboliese tempo toon dat hulle byna ses keer soveel voedsel benodig. Anders as by arende veroorsaak die sosiale gedrag van rooikatte dat hulle getalle kan vermeerder as dassies volop word. Die digtheidskattings vir ander dele van die Kaapprovinsie dui moontlik op die onderste en boonste grense t.o.v. die wisseling in rooikatgetalle. Langtermyn-vangste van rooikatte op plase toon dat hulle getalle kan toeneem met sowat 22% en kan afneem met sowat 34% as reaksie op reënval, met 'n tydvertraging van 6-12 maande. Dassies kan meer as 50% van rooikatte se voedsel uitmaak, maar geen dassiereste is gevind in 100 ketels wat in hierdie studie ontleed is nie: as ongespesialiseerde roofdiere het die rooikatte hoofsaaklik mak en wilde hoefdiere gevang. Sekondêre roofdiere kom in digthede (ses per 24 $km^2$) voor wat 'n betekenisvolle bedreiging vir jong rooikatte kan inhou.

Voedingseksperimente en metaboliese voorspellings toon dat 'n gemiddelde witkruisarend 1500-1700 $kJd^{-1}$ voedingsenergie in gevangenskap benodig, waarvan ongeveer 75% gemetaboliseer word. Indien 40% van die voedsel verlore gaan, voldoen sowat 500g dassie per dag aan hierdie metaboliese behoefte. Terwyl kuikens in die natuur waarskynlik met effens minder voedsel kan oorleef, het wilde volwassenes moontlik tot 25% meer kos nodig. Veldwaarnemings en robot-fotografie by neste het getoon dat volwasse arendpare 0,43 prooi/dag vang buite die broeiseisoen en 0,57 prooi/dag terwyl hulle kuikens het. Arende moes dus elke vyf tot ses dae 'n addisionele prooi-item vang terwyl hulle kuikens voer, maar hierdie syfer het gewissel na gelang van die ouderdom van die kuikens. Hierdie prooivang-tempo is aansienlik laer as dié tydens ander studies van witkruis- en ander groot arende. Die gemiddelde massa van prooidiere in die park (2565g) was egter sodanig groter dat die arende se totale prooivangste (446 $kgy^{-1}$) en totale voedselinname (284 $kgy^{-1}$) vergelykbaar was met dié van die ander studies. Die waargenome voedselinname was egter steeds laer as die voorspelde minima, veral tydens die broeityd. Arende wat baie haas-agtige diere gevang het, het groter voedseliname-tempos gehad. Dit is waarskynlik toe te skryf aan 'n gebrek aan genoeg dassies as prooi. Die vangstempo van arende het nie gewissel na gelang van broei-aktiwiteite of die jagvermoëns van die paar nie. Tydens droogtes en gedurende daardie geddeltes van die dag wanneer dassies voed het die arende baie prooidiere na hul neste gebring.

University of Pretoria etd – Davies, R A G (1994)



Dassies het 88% uitgemaak van 3823 voedselreste wat onder arendneste in die studiegebied versamel is. Vergeleke met ander studies van die dieët van witkruis-arende waarvan dieselfde metodes gebruik gemaak is, is hierdie verhouding nie baie hoog nie. Dit weerlê dit die siening dat witkruisarende hoogs spesifiek in hul keuse van prooi is. Robot-fotografie en ander metodes het egter getoon dat dassiereste oorverteenwoordig is in die prooi-reste en dat klein haasagtiges baie sterk onderverteenwoordig is. Die mees waarskynlike witkruisarend-dieëtsamestelling is verkry deur die samevoeging van resultate van verskeie waarnemingsmetodes: dassies het 67% van die dieët uitgemaak (46-83% vir arendpare met betroubare data), terwyl haasagtiges 25%, hoefdiere 4% en roofdiere 2% van die prooigetalle uitgemaak het. Van die prooi het 97% in die grootte-klas 500-4000 g geval. Die hoefdier-prooi-items was hoofsaaklik onvolwasse diere en die arende het hierdie diere waarskynlik vermy weens die gevaar van beserings. Skaaplammers het 1,2% van die prooireste en 3,4% van die prooi by neste op plase uitgemaak. Dit is onbekend hoeveel van hierdie prooi geaas is, maar aas vorm waarskynlik 4-11% van die arende se voedselinname. Arende langs die hoë platorand het, desondanks kleiner territoria, meer alternatiewe prooi-items (hoofsaaklik voëls en reptiele) bekom as arende langs die lae platorand. Behalwe vir hoefdiere wat vermy is, was die prooisamestelling van witkruisarende soortgelyk aan die beskikbaarheid van prooi. Is witkruisarende dus prooi-spesifiek? Dassies was tydens my studie beskerm in hulle skuilings, en hulle lae beskikbaarheid is weerspieel deur die feit dat twee groot, nie-gespesialiseerde roofdierspesies in die park geen dassies in hul dieët gehad het nie. Daar was ook nie tekens van 'n verandering in die dieëtsamestelling van arende tydens die toename in getalle van klipkonyne nie. Daar kan dus afgelei word dat witkruisarende spesialisroofdiere is wat dassies vang ten spyte van hierdie prooi se relatiewe lae beskikbaarheid.

Die erupsie en slytasie van die tande in 3359 dassie-maksillae uit arend-prooi in die KRNP en nog 2259 maksillae elders uit die Kaapprovinsie is gebruik om die geslags- en ouderdomsamestelling van dassie-prooi te bepaal, en dit is met die geslags- en ouderdomsamestelling van die bevolking in die park vergelyk. Baie jong dassies is deur die arende vermy, waarskynlik weens lae voedselwaarde (1/16 van die volwasse massa). Arende het een-tot-twee-jaar-oue dassies verkies wat die grootste enkele ouderdomsklas van die bevolking uitgemaak het. Hulle het betekenisvol meer onvolwasse mannetjie-dassies as wyfies gevang: dit het 'n ongelyke geslagsverhouding onder volwasse dassies tot gevolg gehad. Verstrooiing van onvolwasse mannetjie-dassies kom dikwels voor en hierdie diere is waarskynlik kwesbaar wanneer hulle in vreemde gebiede beweeg sonder die voordele van "brandwagte". Volwasse dassies is vermoedelik beter in staat om arende te ontduik, en hul voorkoms in prooireste weerspieël die bevolkingsamestelling. Arende was egter vir drie uit elke vier mortaliteite onder volwasse en ou dassies verantwoordelik. Ou dassies (8-13 jaar oud) is meer dikwels as verwag deur arende gevang, waarskynlik omdat hulle nie so vinnig kon vlug nie. Die arende het jaarliks sowat 'n derde van hierdie diere gevang. Alhoewel meer ou wyfie dassies beskikbaar was as prooi, vergeleke met ou mannetjies, is daar disproportioneel-baie ou wyfies gevang, waarskynlik omdat wyfie-dassies die "brandwagte" is, terwyl ander faktore bydra tot die dood van mannetjies. Die hoofneigings in prooivoorkoms tussen dassies word dus verklaar deur die kwesbaarheid van verskilende geslags/ouderdomsgroepe en nie deur die aktiewe voorkeur deur arende nie. Hierdie patrone is onderhewig aan groot wisselings met tyd en tussen geografiese gebiede. Dit het gekorreleer met reënval - 'n bewys van die dinamiese dassie-bevolkingstruktuur en die geldigheid van die ouderdomsbepalingstegnieke. Die grootte van volwasse dassies, soos geskat deur maksilla-grootte, het ook gekorreleer met reënval. Arende langs die lae platorand het meer "oortollige" dassies, bv. jong mannetjies en ou wyfies, gevang. Arende langs die hoë platorand het meer "moeilike" prooi gevang, bv. onvolwasse dassies en gesonde teeldiere, bv. volwasse wyfies, asook ander prooispesies. Arende langs die hoë platorand is klaarblyklik blootgestel aan 'n lae dassie:arend verhouding, soos blyk uit die feit dat daar minder dassie-reste oorbly en dat meer dassie-skedels deur die arende oopgeskeur word. 'n Soortgelyke tendens is ook bespeur by data uit ander berggebiede waar daar relatief min dassies is, bv. Fynbos, en tydens tye wanneer dassies in lae getalle voorgekom het, bv. in die oos-Kaap en in die Fynbos gedurende die vroeë 1970's.

Vroeë nesmaak deur arende op plase wys dat hierdie roofvoëls voedselbronne benut het wat ontoeganklik is in die KRNP. Waarnemings by neste toon dat sowat twee arendpare op 'n gemiddelde veeplaas in bergterrein jaarliks 6-13 skaaplammers

University of Pretoria etd – Davies, R A G (1994)



vreet. Dit is nie bekend of hierdie lammers gesond, sterwend of dood was toe hulle deur die arende gevang is nie. Ongeveer 20% van die lammers vrek voor speen-ouderdom, wat sowat 145 lammers/jaar laat wat deur arende op 'n Karoo-plaas geaas kan word. Witkruisarende aas waarskynlik meeste van die lammers wat na neste gebring word, soos blyk uit ander studies op groot arende, bv. die goue arend. Betroubare ontledings van lam-mortaliteit deur predasie kan net gedoen word deur die lykskouing van lammers in die veld tydens lamtyd. Wye opnames van vrektes onder Merino in Australië (baie vergelykbaar met die Karoo) toon dat predasie die oorsaak van dood is by 1,7% van die lammers. Wêreldwye opnames toon verder dat arende verantwoordelik is vir 2,4% van alle predasie. Beperkte opnames in witkruisarend-habitat in Suid-Afrika toon laer verliese weens predasie, waarvan niks aan arende toegeskryf kan word nie. By gebrek aan goeie Suid-Afrikaanse data, wys die Australiese data dat die gemiddelde verlies op 'n Karoo-plaas ongeveer 0,32 lammers per jaar of R24 is - 'n minimale verlies. Waarnemings toon dat die meeste arende in die Karoo natuurlike prooi verkies, waaraan hul as kuikens gewoond raak. In teenstelling met sommige ander groot arendspesies, vergader witkruisarende en breëkoparende nie in gebiede waar skape lam nie. Daar is egter bewyse dat sommige witkruisarende wel lammers vang, en sulke probleme is waarskynlik beperk tot 'n klein getal veeplase. Verliese kan beperk word deur meer intensiewe plaasbestuur: die gebruik van skaapwagters tydens lamtyd, verwydering van karkasse en die lam van skape in kampe waar arende nie jag nie. Die bestuur van vee is goedkoper as die bestuur van roofdiere, bv. die vervoer van arende. Afweer weens slegte smaak mag in die toekoms nuttig wees, maar indiwiduele arende met volgehoue predasie op kleinvee behoort verwyder te word na dieretuine of falkeniere om te verhoed dat hierdie gedrag deur ander arende aangeleer word.

Dassies het tydens my studie 'n lae digtheid en 'n lae beskikbaarheid gehad. Tydens die jare van akkurate dataversameling is gemiddeld 11% (117) van die 1062 dassies per arend-territorium gevang. Die arende het ook 8% van die klipkonyngetalle gevang (11% gedurende 1989). Die predasie deur arende verteenwoordig 27% van die dassie-mortaliteit en vergestalt 29% van die jaarlikse dassie-geboortes. Kernfaktorontleding het getoon dat verandering in die dassiegetalle verbind kon word met predasie, en nie soseer met voedseltekorte of ander effekte t.o.v die lae trofiese vlak nie. Die duur van my studie was waarskylik te kort om digtheidsafhanklike demografiese effekte te toon, maar mortaliteit was meer verwant aan dassie-digtheid as met hul geboortetempo. Voortplanting word vermoedelik weens oorbevolking versteur deur hoë dassie-digthede. Afgesien van wisselings in die dassie-getalle het die arende jaarliks 'n konstante 11% van die dassies gevang. Baie dassies wat gevang is, was uit ouderdomsklasse met 'n hoë oorlewing en het daarom 'n additiewe effek gehad. Arende het dus tydens hierdie studie 'n remmende effek op bevolkingsgroei gehad. Wisselende plantevoedselbeskikbaarheid en 'n dassiebevolking met 'n hoë potensiaal vir toename skep 'n onstabiele toestand: enige faktor met 'n volgehoue remmende effek op bevolkingsgroei speel dus 'n rol om wanbalanse tussen die dassies en hul voedsel te verminder.

Data uit my studie asook uit ander veldstudies is versamel om 'n gedetaileerde en spesifieke bevolkingsmodel saam te stel wat die dassies se demografie gesimuleer het na aanleiding van langtermyn-klimatologiese data vir die Karoo. Hierdie model wyk af van vorige modelle vir dassies deurdat dit die akkurate meting van skuiling en dassie-drakrag van die veld in ag neem, en deurdat dit die verhoging van drakrag weens die jaarlikse reënval en die verlaging van drakrag weens dassie-beweiding in ag neem. Bevolkingsverskynsels in die model word bepaal deur die verhouding van aantal dassies (P) tot dinamiese drakrag (K), sodat 'n klein dassiebevolking na goeie reën 'n minimum-hoeveelheid mortaliteit en 'n maksimum voortplantingstempo getoon het. Groot dassie-bevolkings het tydens droogtes die teenoorgestelde ondervind. Die model wys dat predasie veroorsaak dat dassie-getalle die hele tyd na aan die veld se drakrag is. Die drakrag word op sy beurt weer bepaal word deur reënval-bepaalde nuwe plantegroei binne die 'veilige' area naby dassie-skuilings. Gedokumenteerde bevolkings-'ontploffings' van dassies in die verlede het elke keer saamgeval met voorspelde afnames in dassiegetalle: hierdie dassies het waarskynlik meer opsigtelik geword deur bewegings en verstrooiing weens 'n afnemende voedselbeskikbaarheid en drakrag binne die 'veilige' gebiede vir dassies. Die raaiselagtige afname in dassiegetalle tydens die vroeë 1980's kan toegeskryf word aan goeie groei van plante, gevolg deur 'n knellende droogte. Voorspellings uit die model t.o.v. hierdie bevolkings-afname onder verskillende reënval-toestande het sterk gekorreleer met veld-tellings van dassies in die KRNP, asook in die Matobo heuwels. Reënval-aangedrewe dassie-'uitbrake' is meer waarskynlik in in droeë

University of Pretoria etd – Davies, R A G (1994)



gebiede met 'n wisselende reënval. 'Uitbrake' word volgens die model hoofsaaklik veroorsaak deur oorbeweiding van die habitat, maar die uitroei van roofdiere het waarskynlik grootliks bygedra tot die dassie-'uitbraak' gedurende die 1940's. Kernfaktoronteding en die gesimuleerde verwydering van roofdiere in die model, sowel as kompensatoriese predasie, toon dat roofdiere maklik enige 'surplus'-dassies verwyder, selfs teen hoë dassie-digthede. In die afwesigheid van predasie was mortaliteit weens voedseltekort en die samehangende afname in vrugbaarheid nie genoeg om in tye van hoë dassiegetalle en 'n lae drakrag gereelde 'uitbrake' en, daarna, drastiese afnames in dassiegetalle te verhoed nie. Hierdie voorspellings was konsekwent vir 'n wye reeks van drastiese parameter-veranderings binne die model. Jaarlikse wisseling in die aantal dassies in die 'beskermde' gebiede het 'n digtheidsafhanklike roofdier-prooi interaksie versluier. Die roofdiere het egter steeds prooigetalle beheer in die swak sin deurdat die dassies tot areas met skuiling beperk word en deurdat dassiegetallewisseling bepaal word deur die wisseling van die hoeveelheid voedsel naby skuilings. Uitputting van voedselbronne tydens ernstige droogtes kan groot dassie-emigrasies van 'surplus'-dassies tot gevolg hê, maar die normale getal roofdiere is in staat om hierdie dassies te verwyder. Verwydering van die effekte van arende alleen of rooikatte alleen in die model, het nie groot verskille in die demografie van die dassies veroorsaak nie, maar die teenwoordigheid van beide roofdiere was nodig om die volle beperkende effek op dassie-bevolkings te veroorsaak. Hierdie gevolgtrekking is versterk deur waarnemings op dassies op 'n plaas waar alle roofdiere behalwe witkruisarende uitgeroei is. Dassiebevolkings verskil van die sikliese bevolkings wat elders bestudeer is deurdat die bevolkingsgetalle ongereeld verander onder die invloed van die onvoorspelbare reënval van die Karoo. In teenstelling met die klimaat-beheerde roofdier-prooi stelsels in Australië ontsnap dassies amper nooit die effek van predasie nie. Die unieke eienskap van die witkruisarend-dassie stelsel is toe te skryf aan die effekte van permanente en doeltreffende skuilings, asook aan die buitengewone situsie dat die effektiewe dassiebeskikbaarheid vir roofdiere baie laag is ondanks relatiewe hoë dassiegetalle na reënval.

Hierdie studie, sowel as ander studies elders in Afrika, toon dat witkruisarende hoofsaaklik prooi op klipdassies en dat sterk predasie op volwasse en ou dassies plaasvind. Daarom is dit nie verbasend dat die morfologie asook die gedrag van beide dassies en arende, kenmerke van onderlinge aanpassing toon nie. Beide spesies toon opsigtelike aanpassings t.o.v. hulle omgewing sowel as t.o.v. mekaar. Hiedie aanpassings het waarskynlik hul afhanklikheid van hul berg-habitat versterk. Dassies bestee so min as moontlik tyd weg van hul skuiling om sodoende predasie te vermy, veral op winderige dae wanneer arende baie aktief is. Hulle maak ook gebruik van 'brandwagte' terwyl hulle groepsgewys voed. Arende, daarenteen, jag tydens tye van die dag wanneer dassies weg van skuiling voed. Hulle jag paarsgewys om dubbele aanvalle op hul ontduikende prooi moontlik te maak en om prooi te vang wat in ruigtes skuil. Hulle maak ook gebruik van verskuilde aanvalsmetodes. 'n Spesiale ligskerm in die oë van dassies mag help dat dassies aanvallende arende makliker kan raaksien. Abnormale groot pote van witkruisarende is waarskynlik 'n aanpassing om prooi te vang wat dubbeld so groot is as die prooi van ander vergelykbare arende. Baie aspekte van die arende se lewens-styl, bv. hul duidelike territorialiteit en hul konserwatiewe broeigedrag, hou verband met die ongewone stabiliteit van die dassiegetalle, wat op sy beurt weer verklaar word deur die permanente skuilings en die nabygeleë weidingsareas van dassies. Witkruisarende vang soms lammers, maar dit gebeur so selde dat die skade vir die gemiddelde veeboer in die Karoo minimaal is. Indien boere kla oor probleme betreffende arende, kan hierdie gevalle indiwidueel ondersoek word deur die karkasse van lammers te ontleed vir die ware oorsaak van dood: hierdie benadering is baie meer positief as die ontkenning van die probleem wat dikwels 'n verwydering tussen boere en bewarings-georiënteerdes veroorsaak. Indien arende wel skade aanrig kan bestuurstegnieke aanbeveel word wat die skade sal minimeer of uitskakel. Daar bestaan egter 'n grrot moontlikheid dat die indiwiduele arende onskuldig is en dat hulle deur menslike betrokkenheid 'n opvoedingsgeleentheid aan iemand gebied het. Hierdie studie toon dat die finansiële voordele van arende op 'n plaas in terme van die beskerming van weiding hul nadele kan oorskadu met 'n faktor van 150. Die finansiële voordeel van die bewaring van so 'n voordelige diersoort moet beklemtoon word tydens opvoedingsprojekte, maar hierdie projekte moet nie diersoorte wat minder opsigtelike finansiële en ekologiese voordele inhou, oor die hoof sien nie. Verdraagsaamheid t.o.v. aanpasbare groot roofdiere soos arende is 'n eenvoudige en maklike maatreël wat boere in die Karoo kan tref om die ekologie van die Karoo tot sy vorige kompleksiteit en stabiliteit te herstel.

University of Pretoria etd – Davies, R A G (1994)



# REFERENCES


ACOCKS, J.P.H. 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Africa* 28: 1-192. Govt. Printer, Pretoria.

AKÇAKAYA, H.R. 1992. Population cycles of mammals: evidence for a ratio-dependent hypothesis. *Ecological Monographs* 62: 119-142.

ALEXANDER, G. 1964. Lamb survival: physiological considerations. *Proc. Aust. Soc. Anim. Prod.* 5: 113-122.

ALFORD, J.R. & BOLEN, E.G. 1972. A note on golden eagle talon wounds. *Wilson Bull.* 84: 487-489.

ALI, S. & RIPLEY, S.D. 1969. *Handbook of the birds of India and Pakistan*. Oxford University Press, Bombay.

ALLAN, D.G. 1984. Black eagles in the Magaliesberg. *Bokmakierie* 36: 55-57.

ALLAN, D.G. 1987. Report on bustard research done at the Karoo National Park in November 1987. Unpubl. mimeograph, Percy Fitzpatrick Institute, University of Cape Town.

ALLAN, D.G. 1988. Breeding success, nest spacing and territory size of black eagles in the Magaliesberg, South Africa. *Gabar* 3: 76-81.

ALLAN, D.G. 1989. Strychnine poison and the conservation of avian scavengers in the Karoo, South Africa. *S. Afr. J. Wildl. Res.* 19: 102-106.

ALLARDICE, R. & ERASMUS, R. 1989. Problem animal control: black eagle *Aquila verreauxii*. W. Fourie, Perdebond. Unpubl. mimeograph, January 1989, Report to the Director, Cape Dept. Nat. Environ. Cons., Cape Town. 4pp.

ALLEN, P.M. 1976. Evolution, population dynamics, and stability. *Proc. Nat. Acad. Sci. USA* 73: 665-668.

AMBROSE, H.W. 1972. Effect of habitat familiarity and toe clipping on rate of owl predation in *Microtus pennsylvanicus*. *J. Mammal.* 53: 909-912.

ANDREWS, P. 1990. *Owls, caves and fossils*. Natural History Museum Publications, London.

ANDREWS, R.D. & BOGGESS, E.K. 1978. Ecology of coyotes in Iowa. pp. 249-265. In: *Coyotes - biology, behavior, and management*, (ed.) M. Bekoff, Academic Press, New York.

ANGERBJÖRN, A. 1983. Reliability of pellet counts as density estimates of mountain hares. *Finn. Game Res.* 41: 13-20.

ANGERBJÖRN, A. 1989. Mountain hare populations on islands: effects of predation by red fox. *Oecologia* 81: 335-340.

ANON. 1965. Annual report for 1964-65 from the Wool Research Laboratory, Agricultural Research Station, Trangie, N.S.W.

ANON. 1968. Agricultural research in the south-east of South Australia and adjacent areas of Victoria. C.S.I.R.O. Aust., Melbourne.

ANON. 1970. *The Edinburgh world atlas*. John Bartholomew & Son Ltd., Edinburgh. 159pp.

ANON. 1985. *Agriculture in R.S.A.* Dept. Agric., Pretoria.

ANON. 1987. *Eagles and farmers*, (ed.) D. Butchart, Endangered Wildl. Trust & S. Afr. Ornithol. Soc., Johannesburg. 29pp.

ANON. 1992a. Minutes of Cockscomb Farmers Association open day, Kleinpoort August 1992, unpubl. mimeograph.

ANON. 1992b. Quarterly estimates of livestock numbers. August 1992. Dept. Agric., Pretoria.

ANSELL, W.F.H. 1960. *Mammals of Northern Rhodesia*. Lusaka: Government Printer.

ARDITI, R. & SAÏAH, H. 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* 73: 1544-1551.

ARMENTROUT, D. 1980. Environmental viewpoint. pp. 6-9. In: Proc. of the Predator Control Summit. Texas Dep. Agric., Austin, Texas.

ARMITAGE, K.B. 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring. *Am. Nat.* 129: 501-519.

ARNOLD, L.W. 1954. *The golden eagle and its economic status*. U.S. Fish & Wildl. Serv. Circular 27. 55pp.

AVERY, D.M. 1992. Ecological data on micromammals collected by barn owls *Tyto alba* in the West Coast National Park, South Africa. *Israel J. Zool.* 38: 385-397.

BAILEY, V.A., NICHOLSON, A.J. & WILLIAMS, E.J. 1962. Interaction between hosts and parasites when some host individuals are more difficult to find than others. *J. theor. Biol.* 3: 1-18.

BAKKER, R.T. 1983. The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. pp. 350-382. In: *Coevolution*, (eds.) D.J. Futuyma & M. Slatkin, Sinauer Associates Inc., Sunderland, Massachusetts. 555pp.

BALLAM, J.M. 1984. The use of soaring by the red-tailed hawk (*Buteo jamaicensis*). *Auk* 101: 519-524.

BALLARD, W.B., WHITMAN, J.S. & GARDNER, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* 98: 54pp.

BALLARD, W.B., WHITMAN, J.S. & REED, D.J. 1990. Population dynamics of moose in south-central Alaska. *Wildl. Monogr.* 114: 49pp.

BALSER, D.S. 1974. An overview of predator-livestock problems with emphasis on livestock losses. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 39: 292-300.

BANFIELD, A.W.F. 1947. A study of the winter feeding habits of the short-eared owl (*Asio flammeus*) in the Toronto region. *Can. J. Res.* 25D: 45-65.

BARASH, D.P. 1974. The evolution of marmot societies: a general theory. *Science* 185: 415-420.

BEACHAM, T.D. 1979. Selectivity of avian predation in declining populations of the vole *Microtus townsendii*. *Can. J. Zool.* 57: 1767-1772.

BEDNARZ, J.C. 1988. Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science* 239: 1525-1527.

BEECHAM, J.J. & KOCHERT, M.N. 1975. Breeding biology of the golden eagle in southwestern Idaho. *Wilson Bulletin* 87: 506-513.

BERGO, G. 1987. Eagles as predators on livestock and deer. *Fauna Norvegica Series C.* 10:95-102.

BERGERUD, A.T., WYETT, W. & SNIDER, B. 1983. The role of wolf predation in limiting a moose population. *J. Wildl. Mgmt* 47:977-988.

BERRYMAN, A.A. 1992. The origins and evolution of predator-prey theory. *Ecology* 73: 1530-1535.

University of Pretoria etd – Davies, R A G (1994)



BERTRAM, B.C.R. 1978. Living in groups: predators and prey. pp 64-96 In: *Behavioural Ecology, an Evolutionary Approach*, (eds.) J.R. Krebs & N.B. Davies, Blackwell, Oxford. 494pp..

BEYNON, P. & RASA, O.A.E. 1989. Do dwarf mongooses have a language?: warning vocalisations transmit complex information. *S. Afr. J. Sci.* 85: 447-450.

BIGALKE, R.C. 1970. Observations on springbok populations. *Zool. Afr.* 5: 59-70.

BIRD, D.M. & HO, S.K. 1976. Nutritive values of whole animal diets for captive birds of prey. *Raptor Res.* 10: 45-49.

BLANCO, J.C. & HIRALDO, F. 1991. On the influence of the red kite (*Milvus milvus* L.) on the small game in a mediterranean area of southern Spain. In: *Global Trends in Wildlife Management* (Trans. 18th Int. Union Game Biol. Congr.). Vol. 2, (eds.) .B. Bobek, K. Perzanowski & W.L. Regelin, Swiat Press, Kraków - Warszawa.

BLOM, C.D. 1981. Group classification of karoo plants. Agricultural Research Institute for the Karoo region, Grootfontein Agricultural College, Middelberg, Cape Province. 18pp.

BOEKER, E.L. & RAY, T.D. 1972. Golden eagle population studies in the south west. *Condor* 73: 463-467.

BOGGESS, E.K., ANDREWS, R.D. & BISHOP, R.A. 1978. Domestic animal losses to coyotes and dogs in Iowa. *J. Wildl. Mgmt* 42: 362-372.

BOLEN, E.G. 1975. Eagles and sheep: a viewpoint. *J. Range Mgmt* 28: 11-17.

BORTOLOTTI, G.R. 1984. Trap and poison mortality of golden and bald Eagles. *J. Wildl. Mgmt* 48: 1173-1180.

BOSHOFF, A.F. 1978. A distribution, status and feeding habit survey of the larger birds of prey and vultures in the Cape Province. Unpubl. Res. Rep. Cape Dept. Nat. Environ. Cons., Cape Town.

BOSHOFF, A.F. 1980. Some socio-economic aspects of a bird of prey questionnaire survey. *S. Afr. J. Wildl. Res.* 10: 71-81.

BOSHOFF, A.F. & FABRICIUS, C. 1986. Black eagles nesting on man-made structures. *Bokmakierie* 38: 67-70.

BOSHOFF, A.F. & PALMER, N.G. 1980. Macro-analysis of prey remains from martial eagle nests in the Cape Province. *Ostrich* 51: 7-13.

BOSHOFF, A.F. & PALMER, N.G. 1988. Black eagle nest spacing and estimated territory size in a karoo habitat. *S. Afr. J. Wildl. Res.* 18: 67-69.

BOSHOFF, A.F., PALMER, N.G. & AVERY, G. 1990. Regional variation in the composition, diversity and species richness of martial eagle prey in the Cape Province. *S. Afr. J. Wildl. Res.* 20: 57-68.

BOSHOFF, A.F., PALMER, N.G., AVERY, G., DAVIES, R.A.G. & JARVIS, M.J.F. 1991. Biogeographical and topographical variation in the prey of the black eagle in the Cape Province, South Africa. *Ostrich* 62: 59-72.

BOSHOFF, A.F., ROUS, R.C. & VERNON, C.J. 198 . Prey of the tawny eagle in the Colesburg district, Cape Province. *Ostrich* 52: 187-188.

BOSHOFF, A.F. & VERNON, C.J. 1980. The distribution and status of some eagles in the Cape Province. *Ann. Cape Prov. Mus. (Nat. Hist.)* 13(9): 106-132.

BOSHOFF, A.F. & VERNON, C.J. 1988. The translocation and homing ability of problem eagles. *S. Afr. J. Wildl. Res.* 18: 38-40.

BOTHA, J.P. 1939. Verteerbaarheid en voedingswaarde van karooweiplante. *Fmg S. Afr.* 54.

BOTHMA, J. du P. 1965. Random observations on the food habits of certain *Carnivora* (*Mammalia*) in southern Africa. *Fauna & Flora (Pretoria)* 16: 16-22.

BOTHMA, J. du P. 1971. Order Hyracoidea. In: *The Mammals of Africa, an Identification Manual*, (eds.) J. Meester & H.W. Setzer, Smithsonian Institution Press, Washington.

BOUTIN, S. 1992. Predation and moose population dynamics: a critique. *J. Wildl. Mgmt* 56: 116-127.

BOWEN, P. 1970. Some observations of the Cape Vulture. *Afr. Wildl.* 24: 125-128.

BOWNS, J.E., DAVENPORT, J.W., WORKMAN, J.F., NIELSON, D.B. & DWYER, D.D. 1973. Determination of cause and magnitude of sheep losses in south-western Utah. *Utah Sci.* 34: 34-37, 52.

BRANCH, B. 1988. Field guide to the snakes and other reptiles of southern Africa. Struik Publishers, Cape Town. 326pp.

BRAND, D.J. 1989. Die beheer van rooikatte (*Felis caracal*) en bobbejane (*Papio ursinus*) in Kaapland met behulp van meganiese metodes. M.Sc. thesis, University of Stellenbosch.

BRAND, D.J. 1992. The use of lithium-chloride as a predation aversion agent for problem eagles in the Cape Province and Orange Free State, South Africa. *Gabar* 7: 51-55.

BRANFIELD, A. 1990. Avian prey of black eagles. *Gabar* 5: 26.

BRETT, L.P., HANKINS, W.G. & GARCIA, J. 1976. Prey-lithium aversions. III: *Buteo* hawks. *Behav. Biol.* 17: 87-98.

BROOKER, M.G. 1974. Field observations of the behaviour of the wedge-tailed eagle. *Emu* 74: 39-42.

BROOKER, M.G. & RIDPATH, M.G. 1980. The diet of the wedge-tailed eagle *Aquila audax* in western Australia. *Aust. Wildl. Res.* 7: 433-452.

BROWER, L.P. 1969. Ecological chemistry. *Sci. Am.* 220: 22-29.

BROWER, L.P. 1984. Chemical defence in butterflies. pp. 109-134. In: *The Biology of Butterflies*, (eds.) R.I. Vane-Wright & P.R. Ackery, Academic Press, London.

BROWER, L.P. RYERSON, W.N., COPPINGER, L.L. & GLAZIER, S.C. 1968. Ecological chemistry and the palatability spectrum. *Science* 161: 1349-1351.

BROWN, C.J. 1988a. Scavenging raptors on farmland. *Afr. Wildl.* 42: 103-105.

BROWN, C.J. 1988b. Home ranges of black eagles in the Natal Drakensberg. *S. Afr. J. Wildl. Res.* 18: 120-125.

BROWN, C.J. 1988c. A study of the bearded vulture *Gypaetus barbatus* in southern Africa. Ph.D. thesis, University of Natal, Pietermaritzburg.

BROWN, C.J. 1991. Declining martial *Polemaetus bellicosus* and tawny *Aquila rapax* eagle populations and causes of mortality on farmlands in central Namibia. *Biological Conservation* 56: 49-62.

BROWN, C.J. & PLUG, I. 1990. Food choice and diet of the bearded vulture *Gypaetus barbatus* in southern Africa. *S. Afr. J. Zool.* 25: 169-177.

BROWN, D. 1975. A test of randomness of nest spacing. *Wildfowl* 26: 102-103.

BROWN, D. & ROTHERY, P. 1978. Randomness and local regularity of points in a plane. *Biometrica* 65: 115-122.

University of Pretoria etd – Davies, R A G (1994)



BROWN, J.E. 1976. Field criteria for predator damage assessment. *Utah Sci.* 37: 26-30.

BROWN, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 70: 160-169.

BROWN, L.H. 1952. On the biology of the large birds of prey of Embu district, Kenya Colony. *Ibis* 94: 577-620, and 95: 74-114.

BROWN, L.H. 1955. Supplementary notes on the biology of the large birds of prey of Embu district, Kenya Colony. *Ibis* 97: 38-64, 183-221.

BROWN, L.H. 1966. Observations on some Kenya eagles. *Ibis* 108: 531-572.

BROWN, L.H. 1970. *African Birds of Prey*. Houghton Mifflin Company, Boston. 320pp.

BROWN, L.H. 1975. Brown on golden eagles and sheep. In: *Population Status of Raptors*, (eds.) Murphy, J.R. *et al.*, *Raptor Research Report* 3: 129-133.

BROWN, L.H. 1976. *Eagles of the World*. Purnell, London. 224pp.

BROWN, L.H. & AMADON, D. 1968. *Eagles, hawks and falcons of the world*. McGraw-Hill, New York. 945pp.

BROWN, L.H., URBAN, E.K. & NEWMAN, K. 1982. *The Birds of Africa*. Vol. 1. Academic Press, London.

BROWN, L.H. & WATSON, A. 1964. The golden eagle in relation to its food supply. *Ibis* 106: 78-100.

BROWN, R.N., SOUTHWICK, C.H. & GOLIAN, S.C. 1989. Male-female spacing, territorial replacement, and the mating system of pikas (*Ochotona princeps*). *J. Mammal.* 70: 622-627.

BRUNS, E.H. 1970. Winter predation of golden eagles and coyotes on pronghorn antelope. *Can. Field Nat.* 84: 301-304.

BULMER, M.J. 1974. A statistical analysis of the 10-year cycle in Canada. *J. Anim. Ecol.* 43: 701-718.

BURGESS, D. 1963. Carrion crows in northern England. *Agriculture, Lond.* 70: 126-129.

BURGHARDT, G.M. & HESS, E.H. 1966. Food imprinting in the snapping turtle, *Chelydra serpentina*. *Science* 151: 108-109.

BURNHAM, K.P., ANDERSON, D.R. & LAAKE, J.L. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72: 8-202.

BURNS, R.J. 1983a. Coyote predation aversion with lithium chloride: Management implications and comments. *Wildl. Soc. Bull.* 11: 128-133.

BURNS, R.J. 1983b. Microencapsulated lithium chloride bait aversion did not stop coyote predation on sheep. *J. Wildl. Mgmt* 47: 1010-1017.

BURNS, R.J. & CONNOLLY, G.E. 1980. Lithium chloride bait aversion did not influence prey killing by coyotes. *Vert. Pest Control Conf.* 9: 200-204.

BYERS, C.R., STEINHORST, R.K. & KRAUSMAN, P.R. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Mgmt* 48: 1050-1053.

CALABY, J.H. 1951. Notes on the little eagle; with particular reference to rabbit predation. *Emu* 51: 33-56.

CARLQUIST, S. 1965. *Island Life*. New York Natural History Press, New York.

CARO, T.M. & FITGIBBON, C.D. 1992. Large carnivores and their prey: the quick and the dead. pp. 117-142. In: *Natural Enemies, the Population Biology of Predators, Parasites and Diseases*. Ed. M.J. Crawley. Blackwell Scientific Publications, Oxford. 576pp.

CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley, London. 235pp.

CDNEC. undated. Bird of Prey Survey - A summary of results from a research project by the Department of Nature and Environmental Conservation, Cape Provincial Administration. 9pp.

CHENEY, C.D., VANDER WALL, S.B. & POEHLMANN, R.J. 1987. Effects of strychnine on the behavior of great horned owls and red-tailed hawks. *J. Raptor Res.* 21: 103-110.

CHENEY, D.L. & SEYFARTH, R.M. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94: 150-166.

CHITTY, D. 1938. A laboratory study of pellet formation in the short-eared owl (*Asio flammeus*). *Proc. Zool. Soc., Lond.* 108A: 267-287.

CHITTY, D. 1960. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38: 99-113.

CHRISTIAN, J.J. 1950. The adreno-pituitary system and population cycles in mammals. *J. Mammal.* 31: 247-259.

CLARK, A.B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* 201: 163-165.

CLUTTON-BROCK, T.H. 1985. Birth sex ratios and the reproductive success of sons and daughters. pp. 221-225, In: *Evolution: essays in honour of John Maynard Smith*, (eds.) P.J. Greenwood, P.H. Harvey, and M. Slatkin, Cambridge University Press, Cambridge.

CLUTTON-BROCK, T.H., MAJOR, M. & GUINNESS, F.E. 1985. Population regulation in male and female red deer. *J. Anim. Ecol.* 54: 831-846.

CLUVER, M.A. 1978. *Fossil reptiles of the South African Karoo*. South African Museum, Cape Town. 54pp.

CODY, M.L. & CODY, C.B.J. 1972. Areal versus lineal territories in the wren, *Troglodytes troglodytes*. *Condor* 74: 477-478.

COE, M.J. 1962. Notes on the habits of the Mount Kenya hyrax (*Procavia johnstoni mackinderi* Thomas). *Proc. Zool. Soc. Lond.* 138: 639-645.

COLLOPY, M.W. 1980. Food consumption and growth energetics of nestling golden eagles. Ph.D. thesis, University of Michigan. 202pp.

COLLOPY, M.W. 1983a. Foraging behavior and success of golden eagles. *Auk* 100: 747-749.

COLLOPY, M.W. 1983b. A comparison of direct observations and collection of prey remains in determining the diet of golden eagles. *J. Wildl. Mgmt* 47: 360-368.

COLLOPY, M.W. 1984. Parental care and the feeding ecology of golden eagle nestlings. *Auk* 101: 753-760.

COLLOPY, M.W. 1986. Food consumption and growth energetics of nestling golden eagles. *Wilson Bull.* 98: 445-458.

COLLOPY, M.W. & EDWARDS, T.C.(jnr.) 1989. Territory size, activity budget, and role of undulating flight in nesting golden eagles. *J. Field Ornithol.* 60: 43-51.

CONNOLLY, G.E. 1978. Predator control and coyote populations: a review of simulation models. pp. 327-345. In: *Coyotes - biology, behavior, and management*, (ed.) M. Bekoff, Academic Press, New York.

University of Pretoria etd – Davies, R A G (1994)


CONWRIGHT-SCHREINER, S.C. 1925. *The migratory springbucks of South Africa*. Fisher Unwin, London.

COOPER, A.B. 1969. Golden eagle kills red deer calf. *J. Zool. (Lond.)* 158: 215-216.

COTTRELL, J.A. 1970. *Black eagle fly free*. Purnell & Sons, Cape Town.

COWAN, D.P. 1987. Aspects of the social organisation in the European wild rabbit. *Ethol.* 75: 197-210.

COWAN, D.P. & BELL, D.J. 1986. Leporid social behaviour and social organization. *Mammal Rev.* 16: 169-179.

COWDEN, J. 1969. Adventures with South Africa's black eagles. *Nat. Geogr.* 136: 532-543.

COWLING, R.M. 1986. A description of the karoo biome project. *S. Afr. Nat. Sci. Prog. Report No. 122*. CSIR, Pretoria. 43pp.

CRAIGHEAD, F.C., Jr., & CRAIGHEAD, J.J. 1956. *Hawks, owls, and wildlife*. Stackpole Co., Harrisburg, and Wildlife Management Institute, Washington. 443pp.

CRAMP, S. & SIMMONS, K.E.L. (Eds.) 1980. *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic. Vol II. Hawks to Bustards*. Oxford University Press.

CRAWLEY, M.J. (Ed.) 1992. *Natural Enemies - The Population Biology of Predators, Parasites and Diseases*. Blackwell, Oxford. 576pp.

CRÊTE, M., TAYLOR, R.J. & JORDAN, P.A. 1981. Optimization of moose harvest in southwestern Québec. *J. Wildl. Mgmt* 45: 598-611.

CURIO, E. 1976. *The Ethology of Predation*. Springer-Verlag, Berlin.

DAVENPORT, J.W., BOWNS, J.E., WORKMAN, J.P. & NIELSEN, D.B. 1973. Assessment of sheep losses. pp. 3-17. In: *Final Report to the Four Corners Regional Commission on Predator Control study*, (ed.) F.H. Wagner, Utah State Univ., Logan. 47pp.

DAVIES, H.L. 1964. Lamb losses in south-western Australia. *Proc. Aust. Soc. Anim. Prod.* 5: 107-112.

DAVIES, R.A.G. 1985. A comparison of springbok *Antidorcas marsupialis* and Merino sheep *Ovis aries* on karoo veld. M.Sc. thesis, University of Pretoria.

DAVIES, R.A.G. 1988. Problem eagles and conservation solutions. *Gabar* 3: 60-66.

DAVIES, R.A.G. 1989. Predation attempt by booted eagle on juvenile rock dassie. *Gabar* 4: 18-19.

DAVIES, R.A.G. & SKINNER, J.D. 1986. Spatial utilisation of an enclosed area of the Karoo by springbok *Antidorcas marsupialis* and Merino sheep *Ovis aries* during drought. *Trans. Roy. Soc. S. Afr.* 46: 115-132.

DAVIES, R.A.G. & VOGEL, J.C. 1992. Radiocarbon dating of sticks from a black eagle nest in the Karoo, South Africa. *Gabar* 7: 24-25.

DAVIS, D.E. (Ed.) 1982. *CRC handbook of census methods for terrestrial vertebrates*. CRC Press, Boca Raton, Florida.

DAWKINS, R. & KREBS, J.R. 1979. Arms races between and within species. *Proc. R. Soc. Lond.* 205: 489-511.

DE GRAAFF, G., ROBINSON, G.A., VAN DER WALT, P.T., BRYDEN, B.R. & VAN DER HOVEN, E.A. 1979. *The Karoo National Park, Beaufort West*. National Parks Board, Pretoria.

DENNIS, S.M. 1969. Predators and perinatal mortality of lambs in western Australia. *Aust. vet. J.* 45: 6-9.

DICKMAN, C.R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* 73: 313-322.

DIJKSTRA, C., DAAN, S. & BUKER, J.B. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology* 4: 143-147.

DIXON, J.B. 1937. The golden eagle in San Diego County California. *Condor* 39: 49-56.

DONÁZAR, J.A. & CEBALLOS, O. 1989. Selective predation by eagle owls *Bubo bubo* on rabbits *Oryctolagus cuniculus*: Age and sex preferences. *Ornis scandinavica* 20: 117-122.

DORRANCE, M.J. & ROY, L.D. 1976. Predation losses of domestic sheep in Alberta. *J. Range Mgmt* 29: 457-460.

DOWNHOWER, J.F. & ARMITAGE, K.B. 1971. The yellow-bellied marmot and the evolution of polygamy. *Am. Nat.* 105: 355-370.

DRENT, R.H., EBBINGE, B. & WEIJAND, B. 1978. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. *Verhandlungen Ornithologisches Gesellschaft Bayern* 23: 239-264.

DUMKE, R.T. & PILS, C.M. 1973. Mortality of radio-tagged pheasants on the Waterloo wildlife area. *Dept. Nat. Res.., Wisconsin. Tech. Bull.* 72: 1-52.

DUNN, E. 1977. Predation by weasels *Mustela nivalis* on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46: 633-652.

EARLY, J.O., ROETHELI, J.C. & BREWER, G.R. 1974a. An economic study of predation in the Idaho range sheep industry, 1970-71 production cycle. *Idaho Agric. Exp. Stn., Prog. Rep.* 182. 49pp.

EARLY, J.O., ROETHELI, J.C. & BREWER, G.R. 1974b. An economic study of predation in the Idaho range sheep industry, 1972-73. *Idaho Agric. Exp. Stn., Prog. Rep.* 186. 45pp.

EBENHARD, T. 1988. Introduced birds and mammals and their ecological effects. *Swed. Wildl. Res.* 13: 1-107.

EBERHARDT, L.L. 1968. A preliminary appraisal of line transects. *J. Wildl. Mgmt* 32: 82-88.

EDMINSTER, F.C. 1939. The effect of predator control on ruffed grouse populations in New York. *J. Wildl. Mgmt* 3: 345-352.

ELLIS, D.H. 1979. Development of behavior in the golden eagle. *Wildl. Monogr.* 70: 3-94.

ELLIS, F. & LAMBRECHTS, J.J.N. 1986. Soils. pp. 18-38, In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds.) R.M. Cowling, P.W. Roux & A.J.H. Pieterse, *S. Afr. Nat. Sci. Prog. Report* No. 124. 115pp.

ELTON, C. S. 1927. *Animal Ecology*. Sidgwick & Jackson, London.

ELTON, C.S. & NICHOLSON, M. 1942. The ten-year cycle in numbers of lynx in Canada. *J. Anim. Ecol.* 11: 215-244.

EMLEN, S.T. & ORING, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.

ENDERSON, J.H., TEMPLE, S.A. & SWARTZ, L.G. 1972. Time-lapse photographic records of nesting peregrine falcons. *Living Bird* 11: 113-128.

ENG, R.L. & GULLIAM, G.W. 1962. The predation of goshawks on ruffed grouse on the Cloquet Forest Research Center, Minnesota. *Wilson Bull.* 74: 227-242.

ERLINGE, S. 1987. Predation and noncyclicity in a microtine population in southern Sweden. *Oikos* 50: 347-352.

University of Pretoria etd – Davies, R A G (1994)



ERLINGE, S., GORANSSON, G., HANSSON, L., HOGSTEDT, G., LIBERG, O., NILSSON, I.N., NILSSON, T., VON SCHANTZ, T. & SYLVEN, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* 40: 36-52.

ERLINGE, S., GORANSSON, G., HOGSTEDT, G., JANSSON, G., LIBERG, O., LOMAN, J., NILSSON, I.N., VON SCHANTZ, T. & SYLVEN, M. 1984. Can vertebrate predators regulate their prey? *Am. Nat.* 123: 125-133.

ERLINGE, S., GORANSSON, G., HOGSTEDT, G., JANSSON, G., LIBERG, O., LOMAN, J., NILSSON, I.N., VON SCHANTZ, T. & SYLVEN, M. 1988. More thoughts on vertebrate predator regulation of prey. *Am. Nat.* 132: 148-154.

ERRINGTON, P.L. 1946. Predation and vertebrate populations. *Quart. Rev. Biol.* 21: 144-177.

ERRINGTON, P.L. 1963. The phenomenon of predation. *Am. Scient.* 51: 180-192.

FAIRALL, N. 1980. Growth and age determination in the hyrax *Procavia capensis*. *S. Afr. J. Zool.* 15: 16-21.

FAIRALL, N. 1991. Factors affecting the dynamics of hyrax populations. *Proc. XX$^{th}$ Congr. Int. Union Game Biol.,* (Gödöllö, Hungary), part 1: 372-377.

FAIRALL, N., VERMEULEN, P. & VAN DER MERWE, M. 1986. A general model of population growth in the hyrax, *Procavia capensis*. *Ecological Modelling* 34: 115-132.

FARRELL, P.J. & WOOD, A.J. 1968. The nutrition of the female mink (*Mustela vison*). III. The water requirement for maintenance. *Can. J. Zool.* 46: 53-56.

FARROW, E.P. 1917. On the ecology of the vegetation of Breckland. *J. Ecol.* 5: 1-18.

FEVOLD, H.R. & CRAIGHEAD, J.J. 1958. Food requirements of the golden eagle. *Auk* 75: 312-317.

FILONOV, K.P. 1989. *Ungulates and large predators in wildlife reserves*. (in Russian) Nauka, Moskva.

FITZGERALD, B.M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *J. Anim. Ecol.* 46: 367-397.

FITZGIBBON, C.D. 1990. Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. *Anim. Behav.* 40: 846-855.

FITZGIBBON, C.D. & FANSHAWE, J. 1989. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *J. Zool.* 218: 99-107.

FLANDERS, S.E. 1948. A host-parasite community to demonstrate balance. *Ecology* 29: 123.

FLANDERS, S.E. & BADGLEY, M.E. 1963. Prey-predator interactions in self-balanced laboratory populations. *Hilgardia* 35: 145-183.

FLUX, J.E.C. 1970. Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. *J. Zool., Lond.* 161: 75-123.

FORRESTER, J.W. 1968. *Principles of Systems*. Wright-Allen Press, Cambridge, MA. 210pp.

FOSTER, H.A. & CRISLER, R.E. 1979. Evaluation of golden eagle predation on domestic sheep, Temperance Creek - Snake sheep and goat allotment, Hell's Canyon National Recreation Area, Oregon. U.S. Fish and Wildlife Services, Animal Damage Control Programme (unpubl. mimeograph) 16pp.

FOURIE, L.J. 1983. The population dynamics of the rock hyrax *Procavia capensis* (Pallas, 1766) in the Mountain Zebra National Park. Ph.D. thesis, Rhodes University, Grahamstown.

FOURIE, L.J. & PERRIN, M.R. 1986. Effective methods of trapping and marking rock hyrax. *S. Afr. J. Wildl. Res.* 16: 58-61.

FOURIE, L.J. & PERRIN, M.R. 1987a. Some new data on the reproductive biology of the rock hyrax. *S. Afr. J. Wildl. Res.* 17: 118-122.

FOURIE, L.J. & PERRIN, M.R. 1987b. Social behaviour and spatial relationships of the rock hyrax. *S. Afr. J. Wildl. Res.* 17: 91-98.

FOURIE, P.B. 1977. Acoustic communication in the rock hyrax, *Procavia capensis*. *Z. Tierpsychol.* 44: 194-219.

FRASER, M.W. 1985. Black eagles (R133) dropping tortoise. *Promerops* 168: 9-10.

FRENCH, N.R. & HEASLEY, J.E. 1981. Lagomorphs in the shortgrass prairie. pp. 695-705. In: *Proceedings of the world lagomorph conference*, (eds.) K. Myers & C.D. MacInnes, University of Guelph, Guelph.

FRERE, P.J. 1982. Verreaux's eagle *Aquila verreauxii* eating carrion. *Scopus* 6: 101.

FULLER, T.K. & KEITH, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Mgmt* 44: 583-602.

FUTUYMA, D.J. & SLATKIN, M. (Eds.). 1983. *Coevolution*. Sinauer Associates Inc., Sunderland, Massachusetts. 555pp.

GARGETT, V. 1971. Some observations on black eagles in the Matopos, Rhodesia. *Ostrich* supplement 9: 91-124.

GARGETT, V. 1972. Observations at a black eagle's nest in the Matopos, Rhodesia. *Ostrich* 43: 77-108.

GARGETT, V. 1975. The spacing of black eagles in the Matopos, Rhodesia. *Ostrich* 46: 1-44.

GARGETT, V. 1977. A 13-year population study of the black eagles in the Matopos, Rhodesia, 1964-1976. *Ostrich* 48: 17-27.

GARGETT, V. 1978. Black eagles in protected and unprotected habitats. pp. 96-102. In: Proceedings of the Symposium on African Predatory Birds. Northern Transvaal Ornithological Society, Pretoria.

GARGETT, V. 1980. The black eagles of the Matopos. *Zimbabwe Science News*. 14: 155-159.

GARGETT, V. 1982a. The food requirement of a black eagle chick. *Ostrich* 53: 178-181.

GARGETT, V. 1982b. Synchronous hatching and the Cain and Abel struggle in the black eagle. *Ostrich* 53: 147-150.

GARGETT, V. 1984. The activities and behaviour of black eagle pairs in the Matopos, Zimbabwe. *Proc V$^{th}$ Pan-Afr. Ornithol. Congr.*: 689-705.

GARGETT, V. 1990. *The black eagle, a study*. Acorn Books & Russel Friedman Books, Johannesburg. 279pp.

GARGETT, V. 1993. Territory boundaries and occupancy and related behaviours of black eagles (*Aquila verrreauxii*) in the Matobo Hills. Report to Department of National Parks and Wildlife Management, Zimbabwe, January 1993, (unpubl. mimeograph),142pp.

GARGETT, V. & GROBLER, J.H. 1976. Prey of the Cape eagle owl *Bubo capensis mackinderi* Sharpe, 1899, in the Matopos, Rhodesia. *Arnoldia (Rhodesia)* 8: 1-7.

University of Pretoria etd – Davies, R A G (1994)



GASSAWAY, W.C., BOERTJE, R.D., GRANGAARD, D.V., KELLEYHOUSE, D.G., STEPHENSON, R.O. & LARSEN, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* 120: 5-59.

GASSAWAY, W.C., STEPHENSON, R.O., DAVIS, J.L., SHEPHERD, P.E.K. & BURRIS, O.E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildl. Monogr.* 84: 1-50.

GAUSE, G.F. 1934. *The struggle for existence.* The Williams and Wilkins Co., Baltimore.

GEE, C.K., MAGLEBY, R.S., BAILEY, W.R., GUM, R.L. & ARTHUR, L.M. 1977. Sheep and lamb losses to predators and other causes in the western United States. U.S.D.A. Agr. Econ. Rep. 369.

GEER, T.A. 1981. Factors affecting the delivery of prey to nestling sparrowhawks (*Accipiter nisus*). *J. Zool., Lond.* 195: 71-80.

GEORGE, W. & CROWTHER, G. 1981. Space partitioning between two small mammals in a rocky desert. *Biol. J. Linn. Soc.* 15: 195-200.

GIBB, J. 1981. What determines the numbers of small herbivorous mammals. *N. Z. J. Ecol.* 4: 73-77.

GLOVER, F.A. & HEUGLY, L.G. 1970. Golden eagle ecology in West Texas. Final report to Natl. Audubon Soc. Colorado Co-operative Wildl. Res. Unit, Fort Collins. 84pp.

GOLLEY, F.B., PETRIDES, G.A., RAUBER, E.L. & JENKINS, J.H. 1965. Food intake and assimilation by bobcats under laboratory conditions. *J. Wildl. Mgmt* 29: 442-447.

GORANSSON, G. 1975. Duvhokens *Accipiter gentilis* betydelse for vinterdodligheten hos fasaner *Phasianus colchicus. Anser* 14: 11-22.

GREEN, M.J.B. 1987. Scent marking in the Himalayan musk deer (*Moschus chrysogaster*). *J. Zool.* 1: 721-737.

GRIFFITHS, R.E., CONNOLLY, G.E., BURNS, R.J. & STERNER, R.T. 1978. Coyotes, sheep and lithium chloride. *Vert. Pest Control Conf.* 8: 190-196.

GROBLER, J.H. 1981. Feeding behaviour of the caracal, *Felis caracal* Schreber 1776 in the Mountain Zebra National Park. *S. Afr. J. Zool.* 16: 259-262.

GRUE, H. & JENSEN, B. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. *Dan. Rev. Game Biol.* 11: 1-48.

GURNEY, W.S.C. & NISBET, R.M. 1975. The regulation of inhomogenous populations. *J. Theor. Biol.* 52: 441-457.

HAGEN, Y. 1952. *Rovfuglene og viltpleien.* (Norwegian) Gyldendal Norsk forlag, Oslo.

HALL, J.G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. *Ecology* 41: 484-494.

HALL-MARTIN, A.J. 1976. Dentition and age determination of the giraffe *Giraffe camelopardalis. J. Zool., Lond.* 180: 263-289.

HANSE, W.A. 1962. Inleidende studie van die dassie *Procavia capensis*, sy verhouding tot die boerdery in Suid-Afrika en beheermetodes. pp. 108-121 In: Verslag nr. 19. Departement van Natuurbewaring, Kaapprovinsie, Cape Town.

HANSKI, I. 1990. Density dependence, regulation and variability in animal populations. *Phil. Trans. R. Soc. Lond.* B 330: 141-150.

HANSSON, L. 1984. Predation as the factor causing extended low densities in microtine cycles. *Oikos* 43: 255-256.

HANSSON, L. 1988a. Empiricism and modelling in small rodent research: how to partition efforts. *Oikos* 52: 150-155.

HANSSON, L. 1988b. Grazing impact by small rodents in a steep cyclicity gradient. *Oikos* 51: 31-42.

HANSSON, L. & HENTTONEN, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67: 394-402.

HANSSON, L. & HENTTONEN, H. 1988. Rodent dynamics as community processes. *Trends Ecol. Evol.* 3: 195-200.

HARMATA, A.R. 1982. What is the function of undulating flight display in golden eagles? *Raptor Res.* 16: 103-109.

HARRIS, W.C. 1840. *Portraits of Game and Wild Animals of Southern Africa.* London: Hullmandel and Walton. Facsimile reprint, 1986. Sable Publishers, Cape Town.

HASSELL, M.P. 1976. *The dynamics of competition and predation.* Studies in Biology No. 72. Edward Arnold, London 68pp.

HASSELL, M.P. & MAY, R.M. 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42: 693-726.

HASTINGS, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theor. Pop. Biol.* 12: 37-48.

HAUGE, T.M. & KEITH, L.B. 1981. Dynamics of moose populations in north eastern Alberta. *J. Wildl. Mgmt* 45: 573-597.

HEARD, D.C. 1992. The effect of wolf predation and snow cover on musk-ox group size. *Am. Nat.* 139: 190-204.

HECTOR, D.P. 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. *Ethology* 73: 247-257.

HENRICI, M. 1945. Digestion experiments with fresh karoo plants. *S. Afr. J. Sci.* 41: 213-217.

HENTTONEN, H. 1985. Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. *Oikos* 45: 156-158.

HENTTONEN, H. & JÄRVINEN, A. 1981. Lemmings in 1978 at Kilpisjärvi: population characteristics of a small peak. *Mem. Soc. Fauna Flora Fennica* 57: 25-30.

HENTTONEN, H., OKSANEN, T., JORTIKKA, A. & HAUKISALMI, V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos* 50: 353-365.

HERRERA, E.A. & MACDONALD, D.W. 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). *J. Anim. Ecol.* 58: 667-679.

HERZIG-STRASCHIL, B. 1978. On the biology of *Xerus inauris* (Zimmermann, 1980) (Rodentia, Sciuridae). *Z. Saugetierk.* 43: 262-278.

HESS, E.H. 1973. *Imprinting.* Van Nostrand, Reinhold.

HEWSON, R. 1981. The red fox *Vulpes vulpes* as a scavenger and predator of sheep in west Scotland. Ph.D. thesis, Univ. of Aberdeen.

HEWSON, R. 1984. Scavenging and predation upon sheep and lambs in West Scotland. *J. Appl. Ecol.* 21: 843-868.

HEY, D. 1959. Conservation of birds in the province of the Cape of Good Hope. *Ostrich suppl.* 3: 23-26.

HILBORN, R. 1979. Some long term dynamics of predator-prey models with diffusion. *Ecol. Modell.* 6: 23-30.

University of Pretoria etd – Davies, R A G (1994)



HILTON-TAYLOR, C. 1987. Phytogeography and origins of the karoo flora. pp. 70-95, In: *The karoo biome: a preliminary synthesis. Part 2 - vegetation and history*, (eds.) R.M. Cowling & P.W. Roux, *S. Afr. Nat. Sci. Prog. Report* No. 142. 133pp.

HILTON-TAYLOR, C. & LE ROUX, A. 1989. Conservation status of the fynbos and karoo biomes. In: B.J. Huntley, (ed.). *Biotic Diversity in Southern Africa*. Oxford University Press, Cape Town.

HOCKEY, P.A.R. 1988. The brown locust - war or peace? *S. Afr. J. Sci.* 84: 8-10.

HODGSON, F.D.I. 1986. Geohydrology. pp. 84-91, In: T*he karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds.) R.M. Cowling, P.W. Roux & A.J.H. Pieterse, *S. Afr. Nat. Sci. Prog. Report* No. 124. 115pp.

HOECK, H.N. 1982. Population dynamics, dispersal and genetic isolation in two species of hyrax (*Heterohyrax brucei* and *Procavia johnstoni*) on habitat islands in the Serengeti. *Z. Tierpsychol.* 59: 177-210.

HOECK, H.N. 1989. Demography and competition in hyrax, a 17 years study. *Oecologia* 79: 353-360.

HOECK, H.N., KLEIN, H. & HOECK, P. 1982. Flexible social organisation in hyrax. *Z. Tierpsychol.* 59: 265-298.

HOFFMAN, M.T. & COWLING, R.M. 1987. Plant physiognomy, phenology and demography. pp. 1-34, In: *The karoo biome: a preliminary synthesis. Part 2 - vegetation and history*, (eds.) R.M. Cowling & P.W. Roux, *S. Afr. Nat. Sci. Prog. Report* No. 142. 133pp.

HOFFMAN, M.T. & COWLING, R.M. 1990a. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo - fact or fiction? *S. Afr. J. Sci.* 86: 286-294.

HOFFMAN, M.T. & COWLING, R.M. 1990b. Desertification in the lower Sundays River Valley, South Africa. *J. Arid Environ.* 19: 105-117.

HOLLING, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can. Entomol.* 91: 293-320.

HOLLING, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 1-60.

HOLTER, J.B., TYLER, G. & WALSKI, T.W. 1974. Nutrition of the snowshoe hare (*Lepus americanus*). *Can. J. Zool.* 52: 1553-1558.

HORNOCKER, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monogr.* 21: 1-39.

HOUSTON, D. 1977. The effect of hooded crows on hill sheep farming in Argyll, Scotland. *J. Appl. Ecol.* 14: 17-29.

HUFFAKER, C.B. 1958. Experimental studies on predation. II. dispersion factors and predator-prey osscillations. *Hilgardia* 27: 343-383.

HUFFAKER, C.B., SHEA, K.P. & HERMAN, S.G. 1963. Experimental studies on predation. Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34: 305-330.

HUGHES, D.A. & RICHARD, J.D. 1974. The nesting of the Pacific Ridley turtle *Lepidochelys olivacea* on Playa Nancite, Costa Rica. *Marine Biol.* 24: 97-107.

HUGHES, K.L., HARTLEY, W.J., HAUGHEY, K.G. & McFARLANE, D. 1964. A study of perinatal mortality of lambs from the Oberon, Orange, and Monaro districts of N.S.W. *Proc. Aust. Soc. Anim. Prod.* 5: 92-99.

HUMPHREYS, A.J.B. 1987. Archaeology. pp. 117-133, In: *The karoo biome: a preliminary synthesis. Part 2 - vegetation and history*, (eds.) R.M. Cowling & P.W. Roux,. *S. Afr. Nat. Sci. Prog. Report* No. 142. 133pp.

HUNTLEY, B.J. 1984. Characteristics of South African biomes. In: *Ecological effects of fire in South African ecosystems*, (eds.) P. de V. Booysen & N.M. Tainton, Springer Verlag, Berlin.

HUNTLY, N.J. 1987. Influence of refuging consumers (Pikas: *Ochotona princeps*) on subalpine meadow vegetation. *Ecology* 68: 274-283.

HUNTLY, N.J., SMITH, A.T. & IVINS, B.L. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *J. Mammal.* 67: 139-148.

HUSTLER, K. & HOWELLS, W.W. 1986. A population study of tawny eagles in Hwange National Park, Zimbabwe. *Ostrich* 57: 101-106.

HUSTLER, K. & HOWELLS, W.W. 1987. Breeding periodicity, productivity and conservation of the martial eagle. *Ostrich* 58: 135-138.

HUSTLER, K. & HOWELLS, W.W. 1990. The influence of primary production on a raptor community in Hwange National Park, Zimbabwe. *J. Trop. Ecol.* 6: 343-354.

IMMELMAN, K. 1975. Ecological significance of imprinting and early learning. *Ann. Rev. Ecol. Syst.* 6: 15-37.

INGRAHAM, K.P., LUGINBUHL, R.C., SCHLOTZHAUER, S.D. & WATTS, H. 1988. *SAS/STAT user's guide. Release 6.03*, (ed.) SAS Institute, Cary, N.C. 1028pp.

IVES, A.R. & DOBSON, A.P. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. *Am. Nat.* 130: 431-447.

JANSE VAN RENSBURG, E. 1991. Problem animals - problem people? *Endangered Wildl.* (J. of the Endangered Wildl. Trust, Johannesburg) 7: 3-12.

JÄRVINEN, A. 1985. Predation causing extended low densities in microtine cycles: implications from predation on hole-nesting passerines. *Oikos* 45: 157-158.

JEDRZEJEWSKI, W., JEDRZEJEWSKI, B., OKARMA, H. & RUPRECHT, A.L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieza National Park, Poland. *Oecologia* 90: 27-36.

JENKINS, A.R. 1984. Hunting behaviour and success in a pair of black eagles. *Ostrich* 55: 102-103.

JENKINS, A.R. 1992. A comparison of provisioning rates at peregrine and lanner falcon nests in the Transvaal, South Africa. *Gabar* 7: 11-14.

JENKINS, D., WATSON, A. & MILLER, G.R. 1964. Predation and red grouse populations. *J. Appl. Ecol.* 1: 183-195.

JENKINS, M.A. & JOSEPH, R.A. 1984. 1981 - an extraordinary year for golden eagle 'triplets' in the central Rocky Mountains. *Raptor Research* 18: 111-113.

JOHNSTONE, J. 1966. *The eagle in fact and in fiction*. Quist, London. 160pp.

JONES, C.G. 1981. Abnormal and maladaptive behaviour in captive raptors. pp. 53-59. In: *Recent Advances in the Study of Raptor Disease*, (eds.) J.E. Cooper & A.R. Greenwood,

JONES, R. 1979. Predator-prey relationships with particular reference to vertebrates. *Biol. Rev.* 54: 73-97.

JOOSTE, J.F. 1983. Game farming as a supplementary farming activity in the Karoo. *Proc. Grassld Soc. sth. Afr.* 18: 46-49.

University of Pretoria etd – Davies, R A G (1994)



JORDAN, D.J. & LE FEUVRE, A.S. 1989. The extent and cause of perinatal lamb mortality in three flocks of Merino sheep. *Aust. vet. J.* 66: 198-201.

KALELA, O. 1971. Seasonal differences in habitats of the Norwegian lemming, *Lemmus lemmus* (L.), in 1959 and 1960 at Kilpisjärvi, Finnish Lapland. *Ann. Acad. Sci. fenn. (A IV)* 178: 1-22.

KEITH, L.B. 1974. Some features of population dynamics in mammals. *Int. Congr. Game Biol.* 11: 17-58.

KEITH, L.B., CARY, J.R., RONGSTAD, O.J. & BRITTINGHAM, M.C. 1984. Demography and ecology of a declining snowshoe hare population. *Wildl. Monogr.* 90: 1-43.

KEITH, L.B., TODD, A.W., BRAND, C.J., ADAMCIK, R.S. & RUSCH, D.H. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proc. XIII$^{th}$ Congr. Game Biol. (Atlanta, Georgia)*: 151-175.

KELLERT, S.R. 1985. Public perceptions of predators particularly the wolf and coyote. *Biol. Conserv.* 31: 167-189.

KENWARD, R.E. 1978a. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.* 47: 449-460.

KENWARD, R.E. 1978b. Predation on released pheasants (*Phasianus colchicus*) by goshawks (*Accipiter gentilis*) in central Sweden. *Viltrevy* 10: 79-112.

KEOGH, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.* 13: 89-132.

KIDD, N.A.C. & LEWIS, G.B. 1987. Can vertebrate predators regulate their prey? A reply. *Am Nat.* 130: 448-453.

KIERSTEAD, H. & SLOBODKIN, L.B. 1953. The size of water masses containing plankton blooms. *J. Marine Res.* 12: 141-147.

KING, J.A. 1959. The social behaviour of prairie dogs. *Sci. Am.* 201: 128-140.

KINGDON, J. 1971. *East African Mammals.* Vol. 1. Academic Press, London.

KINGDON, J. 1990. *Island Africa - The Evolution of Africa's Rare Animals and Plants.* Collins, London. 287pp.

KIRKWOOD, J.K. 1981. Feeding captive birds of prey. *Aviculture Magazine* 87: 256-265.

KIRKWOOD, J.K & THOMPSON, K. 1983. Food and energy consumption of some large raptors at the Bristol Zoological Gardens. *Int. Zoo Ybk* 23: 114-117.

KLEBENOW, D.A. & McADOO, K. 1976. Predation on domestic sheep in northeastern Nevada. *J. Range Mgmt* 29: 96-100.

KLEIBER, M. 1961. *The fire of life.* John Wiley, New York.

KLEIBER, M. 1975. *The fire of life: an introduction to animal energetics.* R.E. Krieger, New York.

KLOPFER, P.H. 1963. Behavioural aspects of habitat selection, the role of early experience. *Wilson Bull.* 75: 15-22.

KOFORD, C.B. 1958. Prairie dogs, whitefaces, and blue gamma. *Wildl. Monogr.* 3: 1-78.

KOLBE, F.F. 1967. A plea for dassies. *Afr. Wildl.* 21: 237-248.

KOLBE, F.F. 1983. Dr S.H. Rubidge, on the dassie problem and "Lammervanger" controversy 1933-1954. *The Naturalist* 27(2): 15-19.

KORPIMÄKI, E. 1981. On the ecology and biology of Tengmalm's owl (*Aegolius funereus*) in southern Ostrobothnia and Suomenselkä, western Finland. *Acta Univ. Oul. A 118. 1981. Biol.* 13: 1-84.

KORPIMÄKI, E. 1985a. Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. *Oikos* 45: 281-284.

KORPIMÄKI, E. 1985b. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Ann. Zool. Fennici* 22: 91-104.

KORPIMÄKI, E. 1986. Predation causing sunchronous decline phases in microtine and shrew populations in western Finland. *Oikos* 46: 124-127.

KORPIMÄKI, E. 1993. Regulation of multiannual vole cycles by density-dependent avian and mammalian predation? *Oikos* 66: 359-363.

KORPIMÄKI, E. & NORRDAHL, K. 1989a. Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. *Ann. Zool. Fennici* 26: 389-400.

KORPIMÄKI, E. & NORRDAHL, K. 1989b. Predation of Tengmalm's owls: numeric responses, functional responses and dampening impact on population fluctuations of microtines. *Oikos* 54: 154-164.

KORPIMÄKI, E. & NORRDAHL, K. 1989c. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. *Oikos* 55: 205-215.

KORPIMÄKI, E. & NORRDAHL, K. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals? *Oikos* 62: 195-208.

KORPIMÄKI, E., NORRDAHL, K. & RINTA-JASKARI, T. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* 88: 552-561.

KRALIK, S. 1967. Breeding of the caracal lynx at Brno Zoo. *Int. Zoo Ybk* 7: 132.

KREBS, C.J., GILBERT, B.S., BOUTIN, S. & BOONSTRA, R. 1986. Estimation of snowshoe hare population density from turd transects. *Can. J. Zool.* 63: 565-567.

KRUUK, H. 1970. Interactions between populations of spotted hyenas and their prey species. In: *Animal populations in relation to their food resources* (ed. A. Watson). British Ecological Society Symposium 10: 359-374.

KRUUK, H. 1972a. *The spotted hyena.* Chicago University Press.

KRUUK, H. 1972b. Surplus killing by carnivores. *J. Zool., Lond.* 166: 233-244.

KRUUK, H. 1978. Spatial organisation and territorial behaviour of the European badger, *Meles meles*. *J. Zool., Lond.* 184: 1-19.

KUNKEL, R. 1992. *Ngorongoro.* Harpers & Collins. 314pp.

KUNO, E. 1987. Principles of predator-prey interaction in theoretical, experimental and natural population systems. *Adv. Ecol. Res.* 16: 249-337.

LACK, D. 1954. *The natural regulation of animal numbers.* University Press, Oxford.

LAINE, K. & HENTTONEN, H. 1983. The role of plant production in microtine cycles in northern Fennoscandia. *Oikos* 40: 407-418.

LAMPIO, T. 1952. An experiment in the control of disease in the snow hare. *Riistat. Julk.* 8: 139-142.

University of Pretoria etd – Davies, R A G (1994)



LASIEWSKI, R.C. & DAWSON, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.

LAWSON, D. 1989. The effects of predators on sheep farming in Natal: An opinion survey. *S. Afr. J. Wildl. Res.* 19: 4-10.

LE HOUÉROU, H.N., BINGHAM, R.L. & SKERBEK, W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J. Arid Environ.* 15: 1-18.

LEDGER, J., HOBBS, J. & VAN RENSBURG, D. 1987. First record of black eagles nesting on an electricity transmission tower. *African Wildlife* 41: 60-66.

LEHTI, R.A. 1947. The golden eagle attacking antelope. *J. Wildl. Mgmt* 11: 348-349.

LENSING, J.E. 1978. The feeding ecology of the rock hyrax *Procavia capensis* Pallas 1766, in southern South West Africa. Report of the South West Administration Division of Nature Conservation and Tourism, Windhoek (unpubl. mimeograph).

LENSING, J.E. 1979. Feeding habits of the rock hyrax, *Procavia capensis* (Pallas, 1766), in southern South West Africa. M.Sc. thesis, University of Pretoria.

LENSING, J.E. 1982. Feeding strategy of the rock hyrax and its relation to the rock hyrax problem in southern South West Africa. *Madoqua* 13: 177-196.

LENSING, J.E. & JOUBERT, E. 1976. Intensity distribution patterns for five species of problem animals in South West Africa. *Madoqua* 10: 131-141.

LEON, B. 1981. Aspects of the energy and water metabolism in the rock hyrax *Procavia capensis* and the elephant shrew *Elephantulus edwardi*. Ph.D. thesis, Univ. of Cape Town.

LEOPOLD, A.S. & WOLFE, T.O. 1970. Food habits of nesting wedge-tailed eagles, *Aquila audax*, in south-eastern Australia. *C.S.I.R.O. Wildl. Res.* 15: 1-17.

LESLIE, P.H., & GOWER, J.C. 1960. The properties of a stochastic model for the predator-prey type of interaction between two species. *Biometrika* 47: 219-234.

LETLEY, O.P. 1962. Foods and feeding. *Lammergeyer* 2: 63.

LIBERG, O. 1984. Food habits and prey impact by feral and house based domestic cats in a rural area of southern Sweden. *J. Mammal.* 65: 424-432.

LIDICKER, W.Z., Jr. 1988. Solving the enigma of microtine "cycles". *J. Mammal.* 69: 225-235.

LIMA, S.L. & DILL, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640.

LINDÉN, H. & WIKMAN, M. 1983. Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. *J. Anim. Ecol.* 52: 953-968.

LINDESAY, J.A. 1984. Spatial and temporal rainfall variability over South Africa, 1963 to 1981. *S. Afr. Geog. J.* 66: 168-175.

LINDESAY, J.A. 1988. South African rainfall, the southern osscilation and a southern hemisphere semi-annual cycle. *J. Climatol.* 8: 17-30.

LITTAUER, G.A. & WHITE, R.J. 1981. Sheep and lamb losses in New Mexico, January 1 - May 1, 1981. Department of Agriculture, New Mexico. (Unpubl. mimeograph) 11pp.

LITVAITIS, J.A. & MAUTZ, W.W. 1976. Energy utilisation of three diets fed to a captive red fox. *J. Wildl. Mgmt* 40: 365-368.

LLOYD, D.E.B. 1976. The protection of pheasants in release pens from birds of prey. Brit. Field Sports Soc., London. 12pp.

LLOYD, M. & DYBAS, H.S. 1966a. The periodical cicada problem. I. population ecology. *Evolution* 20: 133-149.

LLOYD, M. & DYBAS, H.S. 1966b. The periodical cicada problem. II. evolution. *Evolution* 20: 466-505.

LOCKHART, J.M. 1976. The food habits, status and ecology of nesting golden eagles in the Trans-Pecos region of Texas. M.Sc. thesis, Sul Ross State University.

LOCKIE, J.D. 1964. The breeding density of the golden eagle and fox in relation to food supply in Wester Ross, Scotland. *Scottish Nat.* 71: 67-77.

LOCKIE, J.D. & STEPHEN, D. 1959. Eagles, lambs and land management on Lewis. *J. Anim. Ecol.* 28: 43-50.

LORENZ, K. 1935. Companions as factors in the bird's environment. In: *Studies in Animal and Human Behaviour.* Vol. 1, translated by R. Martin (1970). Methuen, London.

LORENZ, K. 1937. The companions in the bird's world. *Auk* 54: 245-273.

LORENZ, K. 1973. *Behind the mirror.* Methuen, London.

LOTKA, A.J. 1925. *Elements of physical biology.* Williams & Wilkins, Baltimore.

LOUW, G.N. 1971. Water economy of certain Namib desert animals. *S. Afr. J. Sci.* 67: 119-123.

LOUW, E., LOUW, G.N. & RETIEF, C.P. 1972. Thermolability, heat tolerance and renal function in the dassie or hyrax, *Procavia capensis. Zool. Afr.* 7: 451-469.

LOVE, J.A. 1979. Daily food intake of captive white-tailed eagles. *Bird Study* 26: 64-66.

LOVEGROVE, B. 1993. *The living deserts of southern Africa.* Fernwood Press, Vlaeberg. 224pp.

LUTTICH, S., RUSCH, D.H., MESLOW, E.C. & KEITH, L.B. 1970. Ecology of red-tailed hawk predation in Alberta. *Ecology* 51: 190-203.

McADOO, J.K. & KLEBENOW, D.A. 1978. Predation on range sheep with no predator control. *J. Range Mgmt* 31: 111-114.

McDONALD, J.W. 1966. Variation in perinatal mortality of lambs with age and parity of ewes. *Proc. Aust. Soc. Anim. Prod.* 6: 60-62.

McENEANY, T.P. & JENKINS, M.A. 1983. Bald eagle predation on domestic sheep. *Wilson Bull.* 95: 694-695.

McFARLANE, D. 1964. The effects of predators on perinatal lamb losses in the Monaro, Oberon, and Canberra districts. *Wool Technol. Sheep Breed.* 11: 11-14.

McFARLANE, D. 1965. Perinatal lamb losses. I. An autopsy method for the investigation of perinatal losses. *N. Z. vet. J.* 13: 116-135.

McGAHAN, J. 1967. Quantified estimates of predation by a golden eagle population. *J. Wildl. Mgmt* 31: 496-501.

McHUGH, J.F. & EDWARDS, M.S.H. 1958. Lamb loss investigations at Rutherglen Research Station. *J. Agric. Vict.* 56: 425-438.

McMURTRIE, R. 1978. Persistence and stability of single-species and prey-predator systems in spatially heterogenous environments. *Mathematical Biosciences* 39: 11-51.

University of Pretoria etd – Davies, R A G (1994)



McNAIRN, I.S. & FAIRALL, N. 1984. Metabolic rate and body temperature of adult and juvenile hyrax (*Procavia capensis*). *Comp. Biochem. and Physiol.* 79a: 539-545.

MACLEAN, G.L. 1985. *Robert's birds of southern Africa.* John Voelcker Bird Book Fund, Cape Town. 848pp.

MACLEAN, S.F., Jr., FITZGERALD, B.M. & PITELKA, F.A. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. *Arct. Alp. Res.* 6: 1-12.

MALAN, G. 1991. Cooperative hunting by rednecked falcons. *Gabar* 6: 70-71.

MALCOM, S.B. 1992. Prey defence and predator foraging. pp. 458-475. In: *Natural Enemies - The Population Biology of Predators, Parasites and Diseases*, (ed.) M.J. Crawley (ed.), Blackwell, Oxford. 576pp.

MALHERBE, A.P. 1963. Notes on birds of prey and some others at Boshoek north of Rustenburg during a rodent plague. *Ostrich* 34: 95-96.

MALY, E.J. 1978. Stability of the interaction between *Didinium* and *Paramecium*: effects of dispersal and predator time-lag. *Ecology* 59: 733-741.

MARCSTROM, V., ENGREN, E., CARY, J.R. & KEITH, L.B. 1989. Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Can. J. Zool.* 67: 658-668.

MATCHETT, M.R. & O'GARA, B.W. 1987. Methods of controlling golden eagle depredation on domestic sheep in south-western Montana. *J. Raptor Res.* 21: 85-94.

MATSON, P. & BERRYMAN, A.A. 1992. Special feature: Ratio-dependent predator-prey theory. *Ecology* 73: 1529.

MAUTZ, W.W., WALSKI, T.W. & URBAN, W.E.jr. 1976. Digestibility of fresh frozen versus pelleted browse by snowshoe hares. *J. Wildl. Mgmt* 40: 496-499.

MAY, R. 1989. The chaotic rhythms of life. *New Scient.* 1689: 37-41.

MECH, L.D. 1970. *The wolf: the ecology and behavior of an endangered species*. The Natural History Press, New York. 384pp.

MERRIAM, H.G. & MERRIAM, A. 1965. Vegetation zones around woodchuck burrows. *Can. Field Nat.* 79: 177-180.

MESSIER, F. 1987. Physical condition and blood physiology of wolves in relation to moose density. *Can. J. Zool.* 65: 91-95.

MESSIER, F. 1989. Towards understanding the relationship between wolf predation and moose density in southwestern Québec. pp. 13-25. In: *Wolf-Prey Dynamics and Management,* (eds.) D. Seip, S. Pettigrew & R. Archibald, British Columbia Ministry of Environment, Wildlife Working Report No. 40.

MESSIER, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* 60: 377-393.

MESSIER, F. & CRÊTE, M. 1984. Body condition and population regulation by food resources in moose. *Oecologia (Berlin)* 65: 44-50.

MESSIER, F. & CRÊTE, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65: 503-512.

METZGAR, L.H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.* 48: 387-391.

MIDGLEY, D.C. undated. Kaart: Verspreiding van bruto langtermyn gimmiddelde jaarlikse sêdiment afvoer in $m^3/km^2$. Departement Hidrologiese Navorsing, Professionele verhandeling No 7 and 16, University of the Witwatersrand.

MILFORD, R.V. 1987. Annual maximum wind speeds for South Africa. *The Civil Engineer in South Africa* January 1987: 15-19.

MILLAR, R.P. 1971. Reproduction in the rock hyrax (*Procavia capensis*). *Zool. Afr.* 6: 243-261.

MILLAR, R.P. 1972. Reproduction in the rock hyrax (*Procavia capensis*) with special reference to seasonal sexual activity in the male. D.Phil. thesis, University of Liverpool.

MILLS, M.G.L. unpubl. Predator:prey relationships amongst the larger mammals in the Kalahari and Kruger. International symposium on predator-prey relationships, Zool. Soc. sth. Afr., Pretoria, June 1988 (oral presentation).

MÖHR, J.P. 1982. The karoo caterpillar *Loxostege frustralis* Zeller (Lepidoptera: Pyralidae) in relation to host plants and natural enemies. Ph.D. thesis, Rhodes University, Grahamstown.

MOOLMAN, L.C. 1984. ,n vergelyking van die voedingsgewoontes van die rooikat *Felis caracal* binne en buite die Bergkwagga Nasionale Park. *Koedoe* 27: 121-129.

MOOLMAN, L.C. 1986a. Aspekte van die ekologie en gedrag van die rooikat *Felis caracal*, Schreber, 1776 in die Bergkwagga Nasionale Park en op die omliggende plase. M.Sc. thesis, University of Pretoria.

MOOLMAN, L.C. 1986b. Aspekte van die ekologie en gedrag van die rooikat *Felis caracal* (Schreber 1776) in die Bergkwagga Nasionale Park en op die omliggende plase. *Pelea* 5: 8-21.

MOORE, R.W., DONALD, I.M. & MESSENGER, J.J. 1966. Fox predation as a cause of lamb mortality. *Proc. Aust. Soc. Anim. Prod.* 6: 157-160.

MOORING, M.S. 1993. Predation on a newborn impala by a martial eagle. *Ostrich* 64: 185-186.

MOORS, P.J. 1977. Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (*Mustela nivalis* L.). *Oecologia (Berl.)* 27: 184-202.

MOREAU, R.E. 1950. The breeding seasons of African birds - 1. land birds. *Ibis* 92: 223-267.

MOULE, G.R. 1954. Observations on mortality amongst lambs in Queensland. *Aust. vet. J.* 30: 153.

MOUNTFORD, M.D. 1988. Population regulation, density dependence, and heterogeneity. *J. Anim. Ecol.* 57: 845-858.

MUELLER, H.C. & BERGER, D.D. 1970. Prey preferences in the sharp-shinned hawk: the roles of sex, experience, and motivation. *The Auk* 87: 452-457.

MUNDY, P.J., ROBERTSON, A.S., KOMEN, J. & O'CONNOR, T.G. 1986. Attacks by black eagles on vultures. *Raptor Res.* 20: 61-64.

MURDOCH, W.W. 1970. Population regulation and population inertia. *Ecol.* 51: 497-502.

MURIE, A. 1944. *The wolves of Mount McKinley*. Fauna of the National Parks of the United States. *Fauna Series* 5: 238pp.

MURIE, J.O. 1992. Predation by badgers on Columbian ground squirrels. *J. Mammal.* 73: 385-394.

MURPHY, J.R. 1975. Status of a golden eagle population in central Utah, 1967 - 1973. Population Status of Raptors, Raptor Res. Rep. 3: 91-96.

University of Pretoria etd – Davies, R A G (1994)



MURPHY, J.R. 1976. Eagles and livestock - some management considerations. pp. 307-313 In: Proc. World Conf. on Birds of Prey, Vienna 1975, (ed.) R.D. Chancellor, ICBP, London.

MURRAY, B.G., Jr. 1982. On the meaning of density dependence. *Oecologia* 53: 370-373.

MYERS, K. & PARKER, B.S. 1975. Effect of severe drought on rabbit numbers and distribution in a refuge area in semiarid north-western New South Wales. *Aust. Wildl. Res.* 2: 103-120.

MYERS, K. & SCHNEIDER, E.C. 1964. Observations on reproduction, mortality and behaviour in a small, free-living population of wild rabbits. *C.S.I.R.O. Wildl. Res.* 9: 138-143.

MYKYTOWYCZ, R. 1966. Observations on odoriferous and other glands in the Australian wild rabbit, *Oryctolagus cuniculus* (L.), and the hare, *Lepus europaeus* P, I: The anal gland. *C.S.I.R.O. Wildl. Res.* 11: 11-29.

MYKYTOWYCZ, R. 1968. Territorial marking by rabbits. *Sci. Am.* 218: 116-126.

MYKYTOWYCZ, R. & GAMBALE, S. 1969. The distribution of dung-hills and the behaviour of free-living rabbits, *Oryctolagus cuniculus* (L.) on them. *Forma func.* 1: 333-349.

NAGY, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57: 111-128.

NASS, R.D., LYNCH, G. & THEADE, J. 1984. Circumstances associated with predation rates on sheep and goats. *J. Range Mgmt* 37: 423-426.

NELLIS, C.H., WETMORE, S.P. & KEITH, L.B. 1972. Lynx-prey interactions in central Alberta. *J. Wildl. Mgmt* 36: 320-329.

NELSON, M.E. & MECH, L.D. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildl. Monogr.* 77: 53pp.

NELSON, M.E. & MECH, L.D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *J. Wildl. Mgmt* 50: 471-474.

NESSE, G.E., LONGHURST, W.M. & HOWARD, W.E. 1976. Predation and the sheep industry in California. Univ. of Calif. (Div. Agric. Sci.), Bull. 1878. 63pp.

NETTE, T., BURLES, D. & HOEFS, M. 1984. Observations of golden eagle, *Aquila chrysaetos*, predation on Dall sheep *Ovis dalli dalli* lambs. *Can. Field Nat.* 98: 252-254.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Mgmt* 38: 541-545.

NEWSOME, A.E. 1990. The control of vertebrate pests by vertebrate predators. *Trends Ecol. Evol.* 5: 187-191.

NEWSOME, A.E., PARER, I. & CATLING, P.C. 1989. Prolonged prey suppression by carnivores - predator-removal experiments. *Oecologia* 78: 458-467.

NEWTON, I. 1978. Feeding and development of sparrowhawk *Accipiter nisus* nestlings. *J. Zool.* 184: 465-487.

NEWTON, I. 1979. *Population ecology of raptors.* T. & A.D. Poyser, Berkhamsted. 399pp.

NEWTON, I. 1992. Birds of Prey. pp. 143-162. In: *Natural Enemies, the Population Biology of Predators, Parasites and Diseases*, (ed.) M.J. Crawley, Blackwell, Oxford. 576pp.

NICHOLSON, A.J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2: 132-178.

NIELSON, D.B. & CURLE, D.M. 1970. Predator costs to Utah's range sheep industry. Dep. of Economics, Utah State Univ., Logan. 11p. mimeo.

NIEMEYER, C. 1977 unpubl. Montana golden eagle removal and translocation project. Final Rep. U.S. Fish Wildl. Serv. Area Office, Billings, Montana. 22pp.

NILSSON, I.N., NILSSON, S.G. & SYLVÉN, M. 1982. Diet choice, resource depression and the regular nest spacing of birds of prey. *Biol. J. Linn. Soc.* 18: 1-9.

NOBLE, G.K. 1939. The role of dominance in the social life of birds. *Auk* 56: 263-273.

NORRDAHL, K. 1990. Pyyntialue pikkunisäkäspyynneissä: koko, sijoitus ja pyyntitulosten yleistettävyys. M.Sc. Thesis, University of Helsinki.

NORTON, P.M. & LAWSON, A.B. 1985. Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. *S. Afr. J. Wildl. Res.* 15: 17-24.

NORTON, P.M., LAWSON, A.B., HENLEY, S.R. & AVERY, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *S. Afr. J. Wildl. Res.* 16: 47-52.

O'GARA, B.W. 1978. Sheep predation by golden eagles in Montana. *Proc. Vert. Pest Control Conf.* 8: 206-213.

O'GARA, B.W. 1981. Predation by golden eagles on domestic lambs in Montana. pp. 345-358. In: 1982 Wildlife-Livestock Relationships Symposium: Proc. 10. April 20-22, 1981. For. Wildl. Range Exp. Stn., (eds.) J.M. Peek & P.D. Dalke, Univ. Idaho, Moscow. 614pp.

O'GARA, B.W., BRAWLEY, K.C., MUNOZ, J.R. & HENNE, D.R. 1983. Predation on domestic sheep on a western Montana ranch. *Wildl. Soc. Bull.* 11:253-264.

O'GARA, B.W. & MATCHETT, M.R. 1985 unpubl. Evaluation of scarecrows for frightening golden eagles from lambing bands. Comp. Rep., Montana Coop. Wildl. Res. Unit, Univ. Montana, Missoula. 45pp.

ODUM, E.P. 1971. *Fundamentals of ecology.* W.B. Saunders, Philadelphia.

OKSANEN, L. & OKSANEN, T. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. *Rep. Kevo Subarctic Res. Stat.* 17: 7-31.

OLSEN, J. & GEORGES, A. 1993. Do peregrine falcon fledglings reach independence during peak abundance of their main prey? *J. Raptor Res.* 27: 149-153.

ORIANS, G.H. & PEARSON, N.E. 1979. On the theory of central place foraging. pp. 154-177. In: *Analysis of Ecological Systems*, (eds.) D.J. Horn, R.D. Mitchell & G. R. Stairs, Ohio State University Press, Columbus.

OSBORNE, T.O. 1981. Ecology of the red-necked falcon *Falco chicquera* in Zambia. *Ibis* 123: 289-297.

OWEN-SMITH, N. 1971. Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. *Nature, Lond.* 231: 294-296.

OWEN-SMITH, N. 1977. On territoriality in ungulates and an evolutionary model. *Quart. Rev. Biol.* 52: 1-38.

PALMER, N.G. unpubl. An investigation into the black eagle *Aquila verreauxii* - small stock relationship in the Ladysmith District. Unpubl. report, March 1983, to the Director, Cape Dept. Nat. Environ. Cons., Cape Town. 4pp.

University of Pretoria etd – Davies, R A G (1994)



PALMER, R. 1985 unpubl. Investigation of the diet of *Felis caracal* and *Felis lybica* in the Karoo National Park. B.Sc. Honours (Zoology) project report, University of Pretoria. 23pp.

PALMER, R. & FAIRALL, N. 1988. Caracal and African wildcat diet in the Karoo National Park and the implications thereof for hyrax. *S. Afr. J. Wildl. Res.* 18: 30-34.

PEARSON, E.W. & CAROLINE, M. 1981. Predator control in relation to livestock losses in central Texas. *J. Range Mgmt* 34: 435-441.

PEARSON, O.P. 1966. The prey of carnivores during one cycle of mouse abundance. *J. Anim. Ecol.* 35: 217-233.

PEARSON, O.P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *J. Mammal.* 52: 41-49.

PECH, R.P., SINCLAIR, A.R.E., NEWSOME, A.E. & CATLING, P.C. 1992. Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia* 89: 102-112.

PEDDIE, D.A. 1975. A taxonomic and autecological study of the genus *Pronolagus* in southern Africa. M.Sc. thesis, University of Rhodesia, Salisbury.

PENNYCUICK, C.J. 1972a. *Animal Flight. Studies in Biology 33.* Edward Arnold, London. 68pp.

PENNYCUICK, C.J. 1972b. Soaring performance of some East African birds, observed from a motor-glider. *Ibis* 114: 178-218.

PEPLER, D. 1989. A method for capturing the red rock rabbit *Pronolagus rupestris*. *S. Afr. J. Wildl. Res.* 19: 47.

PEPLER, D. 1990. Reproductive and developmental patterns in Smith's red rock hare, *Pronolagus rupestris*. The newsletter and journal of the IUCN SSC Lagomorph Specialist Group 11: 19.

PERRINS, C.M. & GEER, T.A. 1980. The effect of sparrowhawks on tit populations. *Ardea* 68: 133-142.

PETRIDES, G.A. 1975. Principle foods versus preferred foods and their relation to stocking rate and range. *Biol. Cons.* 7: 161-170.

PHILANDER, S.G.H. 1983. El Nino Southern Oscillation phenomena. *Nature* 302: 295-301.

PHILLIPS, R.L. & BLOM, F.S. 1988. Distribution and magnitude of eagle/livestock conflicts in the western United States. pp. 241-244 In: *Proc. Vertebr. Pest Conf. 13,* (eds.) A.C. Crabb & R.E. Marsh, Univ. of Calif., Davis.

PHILLIPS, R.L., CUMMINGS, J.L. & BERRY, J.D. 1991. Responses of breeding golden eagles to relocation. *Wildl. Soc. Bull.* 19: 430-434.

PHILLIPS, R.L., WHEELER, A.H., LOCKHART, J.M., McENEANEY, T.P. & FORRESTER, N.C. 1990. Nesting ecology of golden eagles and other raptors in Southwestern Montana and Northern Wyoming. United States Department of the Interior Fish and Wildlife Service, Washington, D.C.: Fish & Wildl. Tech. Rep. 26: 13pp..

PICKFORD, P., PICKFORD, B. & TARBOTON, W. 1989. *Southern African birds of prey*. Struik, Cape Town. 228pp.

PICOZZI, N. 1978. Dispersion, breeding and prey of the hen harrier *Circus cyaneus* in Glen Dye, Kincardineshire. *Ibis* 120: 498-509.

PIMENTEL, D., NAGEL, W.P. & MADDEN, J.L. 1963. Space-time structure of the environment and the survival of parasite-host systems. *Am. Nat.* 97: 141-168.

PIMM, S.L. 1987. The snake that ate Guam. *Trends Ecol. Evol.* 2: 293-295.

PITELKA, F.A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. pp. 199-215. In: *Alaskan Arctic Tundra,* (ed.) M.E. Britton, Arct. Inst. North Am. Tech. Pap. 25.

PORTER, C. 1984. Black eagles (R 133) at Roodekranz (Witpoortjie Falls). *Witwatersrand Bird Club News* 125: 18.

PRINGLE, J.A. & PRINGLE, V.L. 1979. Observations on the lynx *Felis caracal* in the Bedford district. *S. Afr. J. Zool.* 14: 1-4.

PUTNAM, R.J. 1984. Facts from faeces. *Mammal Rev.* 14: 79-97.

RABINOWITCH, V. 1968. The role of experience in the development of food preferences in gull chicks. *Anim. Behav.* 16: 425-428.

RABINOWITCH, V. 1969. The role of experience in the development and retention of seed preferences in Zebra Finches. *Behaviour* 33: 222-236.

RAPTOR GROUP. 1982. Timing of vole hunting in aerial predators. *Mammal Rev.* 12: 169-187.

RASA, O.A.E. 1986. Sociability for survival: why dwarf mongooses live in groups. In: *Behavioural Ecology and Population Biology,* (ed.).L.C. Drickamer, I.E.C./Universite Paul Sabatier/Toulouse.

RENKEN, R.B. & WIGGERS, E.P. 1989. Forest characteristics related to pileated woodpecker territory size in Missouri. *The Condor* 91: 642-652.

RETTIG, N.L. 1978. Breeding behavior of the harpy eagle (*Harpia harpyja*). *Auk* 95: 629-643.

REYNOLDS, R.N. & GUSTAD, O.C. 1971. Analysis of statistical data on sheep losses caused by predation in four western states during 1966-1969. U.S. Dep. Inter., Fish & Wildl. Serv., Washington, D.C. 21pp.

RIDPATH, M.G. & BROOKER, M.G. 1986. Age, movements and the management of the wedge-tailed eagle, *Aquila audax,* in arid Western Australia. *Aust. J. Wildl. Res.* 13: 245-260.

RIDPATH, M.G. & BROOKER, M.G. 1987. Sites and spacing of nests as determinants of Wedge-tailed Eagle breeding in arid western Australia. *Emu* 87: 143-149.

ROBEL, R.J., DAYTON, A.D., HENDERSON, F.R., MEDUNA, R.L. & SPAETH, C.W. 1981. Relationships between husbandry methods and sheep losses to canine predators. *J. Wildl. Mgmt* 45: 894-911.

ROBERTS, D.H. 1986. Determination of predators responsible for killing small livestock. *S. Afr. J. Wildl. Res.* 16: 150-152.

ROBERTSON, G. 1987. Effect of drought on a breeding population of wedge-tailed eagles *Aquila audax. Emu* 87: 220-223.

ROBINSON, T.J. 1981. Systematics of the South African *Leporidae*. D.Sc. thesis, University of Pretoria.

ROGERS, J.G., Jr. 1974. Responses of caged red-winged black-birds to two types of repellents. *J. Wildl. Mgmt* 38: 418-423.

ROPER, T.J., SHEPERDSON, D.J. & DAVIES, J.M. 1986. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* 97: 94-117.

ROSKO, L. 1948. Losses of sheep from predatory animals on summer ranges in Iron County, Utah. Ytah Coop. Wildl. Res. Unit Rep. 16pp.

ROUX, P.W. 1960. Fruit production, germination and survival of seedlings. M.Sc. thesis, University of Natal.

University of Pretoria etd – Davies, R A G (1994)



ROUX, P.W. & OPPERMAN, D.P.J. 1986. Soil erosion. pp. 92-111, In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds.) R.M. Cowling, P.W. Roux & A.J.H. Pieterse, *S. Afr. Nat. Sci. Prog. Report* No. 124. 115pp.

ROUX, P.W. & THERON, G.K. 1987. Vegetation change in the Karoo biome. pp. 50-69. In: *The karoo biome: a preliminary synthesis. Part 2 - vegetation and history*, (eds.) R.M. Cowling & P.W. Roux, *S. Afr. Nat. Sci. Prog. Report* No. 142. 133pp.

ROUX, P.W. & VORSTER, M. 1983. Vegetation change in the Karoo. *Proc. Grassld Soc. sth. Afr.* 18: 25-29.

ROUX, P.W., VORSTER, M., ZEEMAN, P.J.L. & WENTZEL, D. 1981. Stock production in the karoo region. *Proc. Grassld Soc. sth. Afr.* 16: 29-35.

ROWE, E.G. 1947. The breeding biology of *Aquila verreauxi* Lesson. *Ibis* 89: 387-410, 576-606.

ROWE-ROWE, D.T. 1975. Predation by black-backed jackals in a sheep farming region of Natal. *J. S. Afr. Wildl. Mange. Assoc.* 5: 79-81.

ROWLEY, I. 1970. Lamb predation in Australia: Incidence, predisposing conditions, and the identification of wounds. *C.S.I.R.O. Wildl. Res.* 15: 79-123.

RUDEBECK, G. 1950, 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* 2: 65-88; and *Oikos* 3: 200-231.

RUDNAI, J. 1974. The pattern of lion predation in Nairobi Park. *E. Afr. Wildl. J.* 12: 213-225.

SALA, O.E. & LAUENROTH, W.K. 1982. Small rainfall events: an ecological role in semi-arid regions. *Oecologia (Berlin)* 53: 301-304.

SALE, J.B. 1965. The feeding behaviour of rock hyrax (genera *Procavia* and *Heterohyrax*) in Kenya. *E. Afr. Wildl. J.* 3: 1-18.

SALE, J.B. 1966a. The habitat of the rock hyrax. *J. E. Afr. Nat. Hist. Soc.* 25: 205-214.

SALE, J.B. 1966b. Daily food consumption and mode of ingestion in the hyrax. *J. E. Afr. Nat. Hist. Soc.* 25: 215-224.

SALE, J.B. 1970a. Unusual external adaptations in the rock hyrax. *Zool. Afr.* 5: 101-113.

SALE, J.B. 1970b. The behaviour of the resting rock hyrax in relation to its environment. *Zool. Afr.* 5: 87-99.

SAMPSON, C.G. 1985. Veld damage in the Karoo caused by its pre-trekboer inhabitants: preliminary observations in the Seacow Valley. First Annual Research Meeting of the Karoo Biome Project. Addo, October 1985.

SAPSFORD, C.W. 1984. Raptor energetics: a perspective. pp. 173-179. In: *Proceedings of the Second Symposium on African Predatory Birds*. Natal Bird Club, Durban. 254pp.

SAPSFORD, C.W. & MENDELSOHN, J. 1984. An evaluation of the use of tritium for estimating daily energy expenditure for wild Black-shouldered Kites *Elanus caeruleus* and Greater Kestrels *Falco rupicoloides*. pp. 183-194. In: *Proceedings of the Second Symposium on African Predatory Birds*. Natal Bird Club, Durban. 254pp.

SCHAEFER, J.M., ANDREWS, R.D. & DINSMORE, J.J. 1981. An assessment of coyote and dog predation on sheep in southern Iowa. *J. Wildl. Mgmt* 45: 883-893.

SCHMIDT-NIELSEN, K. 1983. *Animal physiology adaptation and environment*. Cambridge University Press, Cambridge.

SCHNELL, J.H. 1968. The limiting effects of natural predation on experimental cotton rat populations. *J. Wildl. Mgmt* 32: 698-711.

SCHRIVNER, J.H. & CONNER, J.R. 1984. Costs and returns of Angora goat enterprises with and without coyote predation. *J. Range Mgmt* 37: 166-171.

SCHRIVNER, J.H., HOWARD, W.E., MURPHY, A.H. & HAYS, J.R. 1985. Sheep losses to predators on a California range 1973-1983. *J. Range Mgmt* 38: 418-421.

SCHULZE, G.E. 1983. 'N moontlike verband tussen die Suidelike Ossilasie / El Nino verskynsels en droogtes oor die somerreenvalstrieke van Suid-Afrika. *Weather Bureau S. Afr. Newsl.* 410: 79-84.

SCOTT, J. 1985. *The leopard's tale*. Elm Tree Books, London. 192pp.

SCOTT, T.G. & KLIMSTRA, W.D. 1955. Red foxes and a declining prey population. *Monogr. Univ. S. Illinois*. No. 1.

SERVENTY, D.L. 1974. The wedge-tailed eagle. *Australia's Wildlife Heritage* 4: 1857-1867.

SHERMAN, P.W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. pp. 311-331. In: *Natural Selection and Social Behavior*, (eds.) R.D. Alexander & D.W. Tinkle, Chiron Press, New York. 532pp.

SHOEMAKER, V.H., NAGY, K.A. & COSTA, W.R. 1976. Energy utilization and temperature regulation by jack rabbits (*Lepus californicus*) in the Mojave Desert. *Physiol. Zool.* 49: 364-375.

SHORT, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *J. Appl. Ecol.* 22: 435-447.

SIEGFRIED, W.R. 1963a. A preliminary report on black and martial eagles in the Laingsburg and Philipstown Divisions. Cape Department of Nature Conservation, Investigation Report No. 5.

SIEGFRIED, W.R. 1963b. A preliminary evaluation of the economic status of *Corvidae* and their control on sheep farms in the Great Karoo. Cape Department of Nature Conservation, Investigation Report No. 4.

SIEGFRIED, W.R. 1968. Breeding season, clutch and brood sizes in Verreaux's eagle. *Ostrich* 39: 139-145.

SIH, A., CROWLEY, P., McPEEK, M., PETRANKA, J. & STROHMEIER, K. 1985. Predation, competition, and prey dynamics: A review of field experiments. *Ann. Rev. Ecol. Syst.* 16: 269-311.

SIMMONS, R. 1988. Offspring quality and the evolution of cainism. *Ibis* 130: 339-357.

SIMMONS, R. 1989. Adaptation and constraint in the breeding of subtropical harriers and eagles. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

SIMMONS, R. 1991. Offspring quality and sibling aggression in the black eagle. *Ostrich* 62: 89-92.

SIMPSON, E.H. 1949. Measurement of diversity. *Nature* 163: 688.

SIMPSON, M.J.A. & SIMPSON, A.E. 1982. Birth sex ratios and social rank in rhesus monkey mothers. *Nature* 300: 440-441.

SINCLAIR, A.R.E. 1989. Population regulation in animals. pp. 197-241. In: *Ecological concepts*, (ed.) J.M. Cherrett, Blackwell, Oxford.

SINCLAIR, A.R.E., OLSEN, P. & REDHEAD, T.D. 1990. Can predators regulate small mammal populations?: evidence from house mouse outbreaks in Australia. *Oikos* 59: 382-392.

University of Pretoria etd – Davies, R A G (1994)


SKINNER, J.D. 1979. Feeding behaviour in caracal *Felis caracal*. *J. Zool., Lond.* 166: 233-244.

SKINNER, J.D. 1993. Springbok (*Antidorcas marsupialis*) treks. *Trans. Roy. Soc. S. Afr.* 48: 291-305.

SKINNER, J.D., DOTT, H.M., VAN AARDE, R.J., DAVIES, R.A.G. & CONROY, A.M. 1987. Observations on a population of springbok *Antidorcas marsupialis* prior to and during a karoo drought. *Trans. Roy. Soc. S. Afr.* 46: 191-197.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the southern African sub-region*. University of Pretoria, Pretoria. 771pp.

SKOGLAND, T. 1974. Villreinens habitatatferd, okologiske og sosiale faktorer. *Utrykt progresjons-rapport til DVF.*

SKORUPA, J.P. 1986. Crowned eagle breeding chronology and diet in rainforest. *Gabar* 1: 59.

SLADE, L.M. & HINTZ, H.F. 1969. Comparison of digestion in horses, ponies, rabbits and guinea pigs. *J. Anim. Sci.* 28: 842-843.

SLOBODKIN, L.B. 1968. How to be a predator. *Am. Zool.* 8: 43-51.

SLOBODKIN, L.B. 1992. A summary of the special feature and comments on its theoretical context and importance. *Ecology* 73: 1564-1566.

SMITH, A.T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* 55: 1368-1376.

SMITH, F.E. 1972. Spatial heterogeneity, stability and diversity in ecosystems. In: *Growth by Intussusception, Ecological Essays in Honour of G. Evelyn Hutchinson. Trans. Conn. Acad. Arts Sci.* 44: 309-335.

SMITH, I.D. 1964. Ovine neonatal mortality in western Queensland. *Proc. Aust. Soc. Anim. Prod.* 5: 100-106.

SMITH, I.D. 1965. Reproductive wastage in Merino sheep in semi-arid tropical Queensland. *Aust. J. exp. Agric. Anim. Husb.* 5: 110-114.

SMITH, T.M. & SHUGART, H.H. 1987. Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* 68: 695-704.

SMITHERS, R.H.N. 1971. The mammals of Botswana. *Mus. mem. Natl Mus. Monum. Rhod.* 4: 1-340.

SNOW, D.W. (ed.). 1978. *An Atlas of Speciation in African Non-Passerine Birds*. Trustees of the British Museum (Natural History), London. 390pp.

SNYDER, N.F. & SNYDER, H.A. 1973. Experimental study of feeding rates of nesting Cooper's hawks. *Condor* 75: 461-463.

SOLOMON, M.E. 1976. *Population dynamics*. Edward Arnold, London.

SOUTHERN, H.N. 1954. Tawny owls and their prey. *Ibis* 96: 384-410.

SOUTHERN, H.N. & LOWE, V.P.W. 1982. Predation by tawny owls (*Strix aluco*) on bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*). *J. Zool., Lond.* 198: 83-102.

SPINAGE, C.A. 1973. A review of the age determination of mammals by means of teeth, with special reference to Africa. *E. Afr. Wildl. J.* 11: 165-187.

SPOFFORD, W.R. 1964. The golden eagle in the Trans-Pecos and Edwards Plateau of Texas. Audubon Conservation Report 1. National Audubon Society, New York. 47pp.

SPOFFORD, W.R. 1975. The problems of golden eagles in the west. Population Status of Raptors, Raptor Res. Rep. 3: 127-128.

SQUIRES, V.R. 1975. Ecology and behaviour of domestic sheep (*Ovis aries* ): A review. *Mammal Rev.* 5: 35-57.

St. AMANT, J. 1970. The mathematics of predator-prey interactions. M.A. thesis, Univ. of California, Santa Barbara.

STALMASTER, M.V. & GESSAMAN, J.A. 1982. Food consumption and energy requirements of captive bald eagles. *J. Wildl. Mgmt* 46: 646-654.

STALMASTER, M.V. & GESSAMAN, J.A. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. *Ecol. Monogr.* 54: 407-428.

STEENKAMP, J.D.G. 1975. Guidelines to the use of dental histology in wildlife research. *J. S. Afr. Wildl. Mgmt Assoc.* 5: 89-94.

STERNER, R.T. & SHUMAKE, A. 1978. Coyote damage-control research: a review and analysis. pp. 297-325. In: *Coyotes - biology, behavior, and management*, (ed.) M. Bekoff, Academic Press, New York.

STEWART, P.A. 1970. Weight changes and feeding behavior of a captive-reared bald eagle. *Bird-Banding* 41: 103-110.

STEYN, D. 1980. Reproduction in the hyrax, *Procavia capensis* in relation to environmental factors. M.Sc. thesis, University of Natal, Pietermaritzburg.

STEYN, D. & HANKS, J. 1983. Age determination and growth in the hyrax *Procavia capensis* (*Mammalia: Procaviidae*). *J. Zool., Lond.* 201: 247-257.

STEYN. P. 1982. *Birds of prey of southern Africa*. David Philip, Cape Town. 309pp.

STEYN, P. 1984. Black eagles (R133) dropping tortoises. *Promerops* 162: 12.

STEYN, P. & TREDGOLD, D. 1977. Observations on the Cape eagle owl. *Bokmakierie* 29: 31-42.

STUART, C.T. 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. *Bontebok* 1: 1-58.

STUART, C.T. 1982. Aspects of the biology of the caracal (*Felis caracal* Schreber, 1766) in the Cape Province, South Africa. M.Sc. thesis, University of Natal, Pietermaritzburg.

STUART, C.T. 1984. The distribution and status of *Felis caracal* Schreber, 1776. *Säugetier. Mitteil.* 31: 197-203.

STUART, C.T. 1986. The incidence of surplus killing by *Panthera pardus* and *Felis caracal* in Cape Province, South Africa. *Mammalia* 50: 556-558.

STUART, C.T. 1987a. A few facts on problem-animal control in the Cape Province. *Afr. Wildl.* 41: 58.

STUART, C.T. 1987b. Problem-animal management or mismanagement. *Afr. Wildl.* 41: 54-56.

STUART, C.T., MACDONALD, I.A.W. & MILLS, M.G.L. 1985. History, current status and conservation of large mammalian predators in Cape Province, Republic of South Africa. *Biol. Conserv.* 31: 7-19.

STUART, C.T., STUART, T.D. & BRAACK, H.H. 1987. New mammal records for the Karoo National Park, with notes on several other species. *Koedoe* 30: 133-137.

STUART, D.R.M. 1971. Food preferences of *Pronolagus*. *E. Afr. Wildl. J.* 9: 163.

SVENDSEN, G.E. 1979. Territoriality and behavior in a population of pikas (*Ochotona princeps*). *J. Mammal.* 60: 324-330.

University of Pretoria etd – Davies, R A G (1994)



SVENDSEN, R.S. 1980. Kongeorn *Aquila chrysaetos* angrep sau. *Var Fuglefauna* 3: 20-26.

SWART, J., PERRIN, M.R., HEARNE, J.W. & FOURIE, L.J. 1986. Mathematical model of the interaction between rock hyrax and caracal lynx, based on demographic data from populations in the Mountain Zebra National Park, South Africa. *S. Afr. J. Sci.* 82: 289-294.

TAKAFUJI, A. 1977. The effect of the rate of successful dispersal of a phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot (Acarine: Phytoseiidae) on the persistence in the interactive system between the predator and its prey. *Researches on Population Ecology* 18: 210-222.

TARBOTON, W.R. & ALLAN, D.G. 1984. The status and conservation of birds of prey in the Transvaal. *Transvaal Museum Monograph* 3. 115pp.

TAST, J. & KALELA, O. 1971. Comparisons between rodent cycles and plant production in Finnish Lapland. *Ann. Acad. Sci. fenn. (A IV)* 186: 1-14.

TAYLOR, R.G., WORKMAN, J.P. & BOWNS, J.E. 1979. The economics of sheep predation in south-western Utah. *J. Range Mgmt* 32: 317-321.

TAYLOR, R.H. & WILLIAMS, R.M. 1956. The use of pellet counts for estimating the density of populations of the wild rabbit, *Oryctolagus cuniculus* (L.). *N. Z. J. Sci.* 38b: 236-256.

TAYLOR, R.J. 1984. Predation. Population and community biology series. Chapman & Hall, London. 166pp.

TEMPLE, S. 1972. A portable time-lapse camera for recording wildlife activity. *J. Wildl. Mgmt* 36: 944-947.

TEXAS CROP AND LIVESTOCK REPORTING SERVICE. 1979. Texas sheep and goat losses and marketing practices. Texas Dep. Agric.

THOMAS, A.D. 1946. The Cape dassie. *Afr. Wildl.* 1: 108-111.

THOMPSON, D.Q. 1955. The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. pp. 166-176. In: Trans. XX$^{th}$ North Am. Wildl. Conf.

TIGNER, J.R. & LARSON, G.E. 1977. Sheep losses on selected ranches in southern Wyoming. *J. Range Mgmt* 30: 244-252.

TIGNER, J.R. & LARSON, G.E. 1981. Golden eagles: scavengers and predators on domestic lambs. Pages 359-361. In: *1982 Wildlife-Livestock Relationships Symposium: Proc. 10. April 20-22, 1981. For. Wildl. Range Exp. Stn*, (eds.) .J.M. Peek & P.D. Dalke, Univ. Idaho, Moscow. 614pp.

TINBERGEN, L. 1940. Beobachtungen uber die Arbeitsteilun des Turmfalken (*Falco tinnunculus* L.) wahrend der Fortpflanzungszeit. *Ardea* 29: 63-98.

TINBERGEN, L. 1946. Sperver als Roofvijand van Zangvogels. *Ardea* 34: 1-123.

TINBERGEN, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation in song birds. *Arch. Néerl. Zool.* 13: 265-343.

TJERNBERG, M. 1981. Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. *Holarct. Ecol.* 4: 12-19.

TJERNBERG, M. 1985. Spacing of golden eagle *Aquila chrysaetos* nests in relation to nest site and food availability. *Ibis* 27: 250-255.

TRAUTMAN, C.G., FREDERICKSON, L.F. & CARTER, A.V. 1973. Relationships of red foxes and other predators to populations of ring-necked pheasants and other prey, 1964-71. S. Dakota Dept Game, Fish, & Parks, P-R Prog. Rep., Project W-75-R-9, Job F-8.2-9.

TROSTEL, K., KREBS, C.J., SINCLAIR, A.R.E. & WALTERS, C.J. 1987. Can predation cause the 10-year hare cycle. *Oecologia* 74: 185-192.

TRUSWELL, J.F. 1977. *The geological evolution of South Africa.* Purnell, Cape Town.

TUER, F.V. 1965. Observations on the black eagle. *Honeyguide* 47: 29-33.

TURK, A. & ARNOLD, W. 1988. Thermoregulation as a limit to habitat use in alpine marmots (*Marmota marmota*). *Oecologia* 76: 544-548.

TURNER, A.J. 1965. A survey of neo-natal lamb losses in a western district sheep flock. *Vic. vet. Proc.* 23: 439-444.

TURNER, M.I.M. & WATSON, R.M. 1965. An introductory study on the ecology of hyrax (*Dendrohyrax brucei* and *Procavia johnstoni*) in the Serengeti National Park. *E. Afr. Wildl. J.* 3: 49-60.

TYSON, P.D. 1983. The great drought. *Leadership SA* 2(3): 49-57.

TYSON, R.D. 1986. *Climatic change and variability in southern Africa.* Oxford University Press, Cape Town. 220pp.

U.S. FISH & WILDLIFE SERVICE. 1978. Predator damage in the West: A study of coyote management alternatives. U.S. Dep. Inter., Fish & Wildl. Serv., Washington, D.C.168pp.

UTTENDÖRFER, O. 1939. Die Ernährung der Deutschen Raubvögel und Eulen. Neudamm.

VAN BALLENBERGHE, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. *Swed. Wildl. Res. Suppl.* 1: 431-460.

VAN DER HORST, C.J. 1941. On the size of the litter and the gestation period of *Procavia capensis*. *Science* 93: 430-431.

VAN DER MERWE, M. & SKINNER, J.D. 1982. Annual reproductive pattern in the dassie *Procavia capensis*. *S. Afr. J. Zool.* 17: 130-135.

VAN DER MERWE, P.J. 1938. *Die Noordwaartse beweging van die boere voor die Groot Trek (1770 - 1842).* Van Stockum & Zoon, The Hague.

VAN DOBBEN, W.H. 1952. The food of the Cormorant in the Netherlands. *Ardea* 40: 1-63.

VAN ZYL, A.J. 1992. Do breeding pairs of martial eagles hold "super-normal" territories? *Gabar* 7: 9-10.

VARLEY, G.C. & GRADWELL, G.R. 1960. Key factors in population studies. *J. Anim. Ecol.* 29: 399-401.

VENTER, J.M., MOCKE, C. & DE JAGER, J.M. 1986. Climate. pp. 39-52, In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds.) R.M. Cowling, P.W. Roux & A.J.H. Pieterse, *S. Afr. Nat. Sci. Prog. Report* No. 124. 115pp.

VERHULST, P.F. 1838. Notice sur la loi que la population suite dans son accroissement. *Correspondence Mathematique et Physique* 10: 113-121.

VERME, L.J. 1983. Sex ratio variation in *Odocoileus*: a critical review. *J. Wildl. Mgmt* 47: 573-582.

University of Pretoria etd – Davies, R A G (1994)



VERNON, C.J. 1965. The 1964 black eagle survey of the Matopos, Rhodesia. *Arnoldia* 2: 1-9.

VILJOEN, S. & DAVIS, D. 1973. Notes on the stomach contents analyses of various carnivores in southern Africa. *Annals of the Transvaal Museum* 28: 353-363.

VILLAGE, A. 1982. The home range and density of kestrels in relation to vole abundance. *J. Anim. Ecol.* 51: 413-428.

VISSER, J. 1963. The black eagles of Zuurhoek, Jansenville. *Afr. Wildl.* 17: 191-194.

VISSER, J.N.J. 1986. Geology. pp. 1-17, In: *The karoo biome: a preliminary synthesis. Part 1 - physical environment*, (eds.) R.M. Cowling, P.W. Roux & A.J.H. Pieterse, *S. Afr. Nat. Sci. Prog. Report* No. 124. 115pp.

VOLTERRA, V. 1931. Variations and fluctuations of the number of individuals in animal species living together. Translated from 1928 edition by R.N. Chapman. Animal Ecology. Arno, New York.

VORSTER, M., BOTHA, P. & HOBSON, F.O. 1983. The utilization of karoo veld by livestock. *Proc. Grassld Soc. sth. Afr.* 18: 35-39.

VORSTER, M. & ROUX, P.W. 1983. Veld of the karoo areas. *Proc. Grassld Soc. sth. Afr.* 18: 18-24.

WADE, D.A. 1982. Impacts, incidence and control of predation on livestock in the United States, with particular reference to predation by coyotes. Council Agric. Sci. & Technol., No. 10.

WADE, D.A. AND BOWNS, J.E. 1980. Procedures for evaluating predation on livestock and wildlife. Published jointly by: Texas Agric. Ext. Serv., Texas A and M University, and U.S. Fish and Wildl. Serv. 42pp.

WAGNER, F.H. 1972. Coyotes and sheep. 44th Faculty Honor Lecture. Faculty Assoc., Utah State Univ., Logan. 59pp.

WAGNER, F.H. & PATTISON, L.G. 1973. Analysis of existing data on sheep loss and predator activity. pp. 18-35. In: Final Rep. to the Four Corners Regional Commission on Predator Control study, (ed.) F.H. Wagner, Utah State Univ., Logan. 47pp.

WAGNER, J.C. & BOKKENHEUSER, V. 1961. The mycobacterium isolated from the dassie *Procavia capensis* (Pallas). *Tubercle* 42: 47-56.

WAGNER, J.C., BUCHANAN, G., BOKKENHEUSER, V. & LEVISEUR, S. 1958. An acid-fast bacillus isolated from the lungs of the Cape hyrax, *Procavia capensis* (Pallas). *Nature* 181: 284-285.

WALSKI, T.W. & MAUTZ, W.W. 1977. Nutritional evaluation of three winter browse species of snowshoe hares. *J. Wildl. Mgmt* 41: 144-147.

WATSON, A. & MILLER, G.R. 1971. Territory size and aggression in a fluctuating red grouse population. *J. Anim. Ecol.* 367-383.

WATSON, A. & ROTHERY, P. 1986. Regularity in spacing of golden eagle *Aquila chrysaetos* nests used within years in northeast Scotland. *Ibis* 128: 406-408.

WATSON, J. & LANGSLOW, D.R. 1989. Can food supply explain variation in nesting density and breeding success amongst golden eagles *Aquila chrysaetos*? pp. 181-186. In: *Raptors in the Modern World,* (eds.) B.-U. Meyburg & R.D. Chancellor, WWGBP, Berlin.

WATSON, R.T. 1987. Flight identification of bateleur age classes: a conservation incentive. *Bokmakierie* 39: 37-39.

WATSON, R.T. 1988. The influence of nestling predation on nest site selection and behaviour of the bateleur. *S. Afr. J. Zool.* 23: 143-149.

WATSON, R.T. 1990. Population dynamics of the bateleur in the Kruger National Park. *Ostrich* 61: 5-12.

WEBBER, C.N. 1989. Park was an inland sea. *Custos* 17(12): 15-17.

WEIR, D.N. 1985. Golden eagles and lambs in Badenoch, Highland. *Scott. Birds* 13: 263-267.

WERGER, M.J.A. 1978. The Karoo-Namib region. 231-299pp. In: *Biogeography and ecology of southern Africa,* (ed.) M.J.A. Werger, W Junk, The Hague.

WERGER, M.J.A. 1986. The Karoo and southern Kalahari. pp. 283-359. In: *Ecosystems of the World 12B: Hot Deserts and Arid Shrublands, B,* (eds.) D.W. Goodall, M. Evaneri & I. Noy-Meir, Elsevier, Amsterdam. 451pp.

WHITE, E.G. & HUFFAKER, C.B. 1969. Regulatory processes and population cyclicity in laboratory populations of *Anagosta kühniella* (Zeller) (Lepidoptera: Phycitidae). II. parasitism, predation, competition, and protective cover. *Researches on Population Ecology* 11: 150-185.

WHITE, F. 1983. *The vegetation of Africa*. Unesco, Paris.

WHITE, I.J. unpubl. Aspects of lion's predator:prey relationship with wildebeest and other prey species in the Kruger National Park. International symposium on predator-prey relationships, Zool. Soc. sth. Afr., Pretoria, June 1988 (oral presentation).

WHITE, M. 1973. Description of remains of deer fawns killed by coyotes. *J. Mammal.* 54: 291-293.

WHITFIELD, P. 1985. Raptor predation on wintering waders in south-east Scotland. *Ibis* 127: 544-558.

WHORISKEY, F.G. & FITZGERALD, G.J. 1985. The effects of bird predation on an estuarine stickleback (*Pisces: Gasterosteidae*) community. *Can. J. Zool.* 63: 301-307.

WILEY, R.W. & BOLEN, E.G. 1971. Eagle-livestock relationships: Livestock carcass census and wound characteristics. *Southwest. Nat.* 16: 151-169.

WILLGOHS, J.F. 1961. The white-tailed eagle *Haliaeetus albicilla albicilla* (Linné) in Norway. *Univ. Bergen Aarb., Math.-Naturv. Serv.* 12: 1-212.

WILLIAMSON, D.T. & MBANO, B. 1988. Wildebeest mortality during 1983 at Lake Xau, Botswana. *Afr. J. Ecol.* 26: 341-344.

WOLFF, J.O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* 50: 111-130.

WOOD, D.H. 1980. The demography of a rabbit population in an arid region of New South Wales, Australia. *J. Anim. Ecol.* 49: 55-79.

WOODFORD, W.H. 1966. *A manual of falconry*. A. & C. Black, London.

WOODROFFE, G.L. & LAWTON, J.H. 1990. Patterns in the production of latrines by water voles (*Arvicola terrestris*) and their use as indices of abundance in population surveys. *J. Zool., Lond.* 220: 439-445.

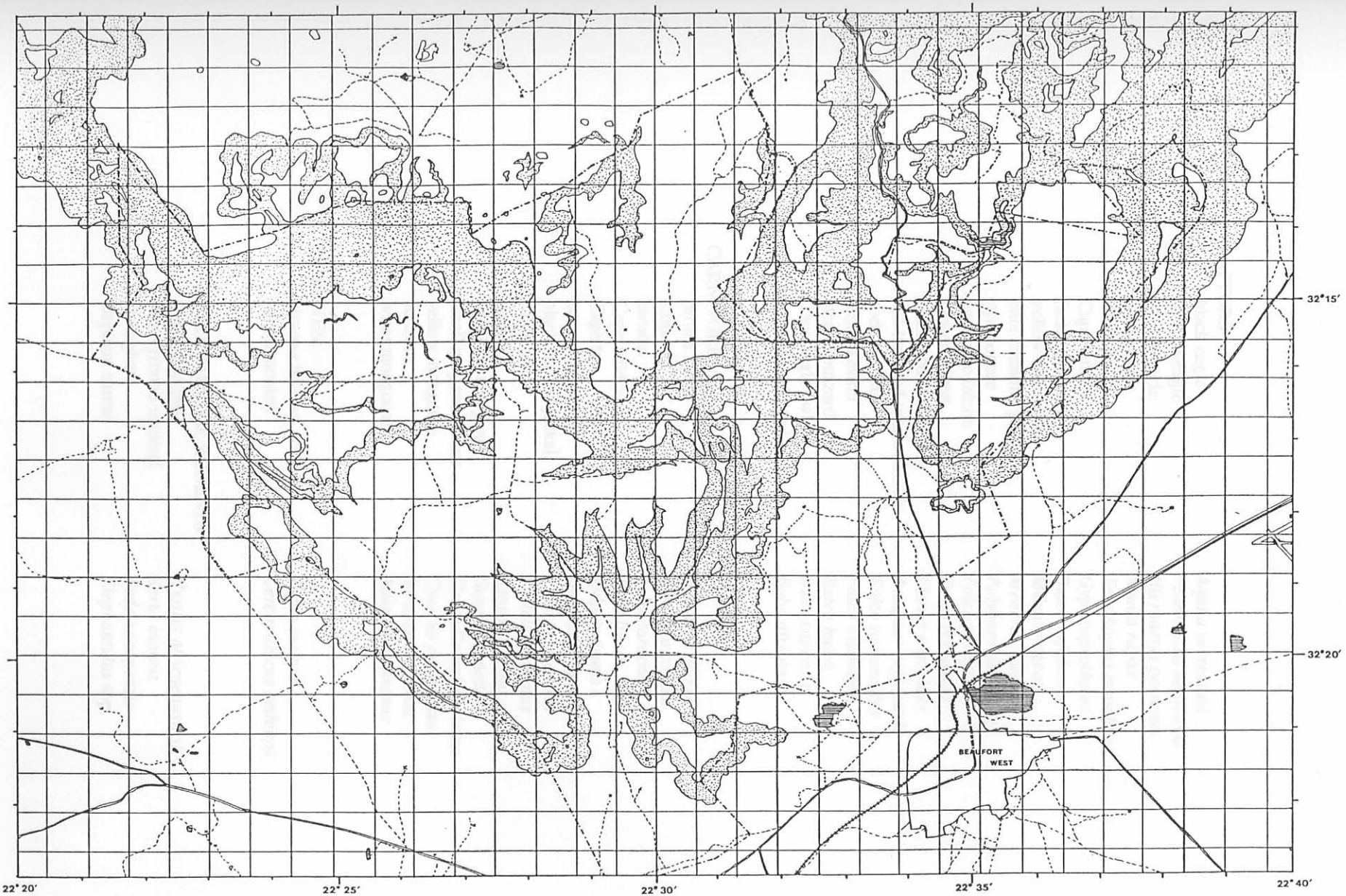
YOM-TOV, Y. In Press. Does the rock hyrax, *Procavia capensis*, conform with Bergmann's rule? *Zool. J. Linn. Soc.* in press.

ZEUNER, F.E. 1963. *A history of domesticated animals*. Hutchinson, London.

University of Pretoria etd – Davies, R A G (1994)



# APPENDIX 1
# DETAILED MAP OF THE KRNP AND ENVIRONS




LEGEND: stippled areas represent mountain slopes as opposed to plains or plateaus; park boundary is shown in alternating dots and dashes; dashed lines represent dirt roads; double lines represent tarmac roads; dams are darkly shaded in horizontal lines; the grid is one kilometer square, and is the same as that used by previous researchers in the park (Branch, Braack, Randall etc.): grid columns are numbered from right to left commencing with the second intact square from the far right (=#1); grid rows are lettered from A (lowest row, partly shown) to X (uppermost row, partly shown).

University of Pretoria etd – Davies, R A G (1994)



# APPENDIX 2
## SPECIES NAMES OF ANIMALS REFERRED TO IN THE THESIS

| | |
|---|---|
| **RAPTORS:** | |
| black eagle | *Aquila verreauxii* |
| martial eagle | *Polemaetus bellicosus* |
| booted eagle | *Hieraaetus pennatus* |
| tawny eagle | *Aquila rapax* |
| bateleur | *Terathopius ecaudatus* |
| Cape vulture | *Gyps coprotheres* |
| jackal buzzard | *Buteo rufofuscus* |
| yellow-billed kite | *Milvus migrans* |
| pale chanting goshawk | *Melierax canorus* |
| gymnogene | *Polyboroides typus* |
| peregrine falcon | *Falco peregrinus* |
| lanner falcon | *Falco biarmicus* |
| black-shouldered kite | *Elanus caeruleus* |
| red-breasted sparrowhawk | *Accipiter rufiventris* |
| rock kestrel | *Falco tinnunculus* |
| lesser kestrel | *Falco naumanni* |
| steppe buzzard | *Buteo buteo* |
| Cape eagle owl | *Bubo capensis* |
| spotted eagle owl | *Bubo africanus* |
| **CARNIVORES:** | |
| brown hyena | *Hyaena brunnea* |
| leopard | *Panthera pardus* |
| caracal | *Felis caracal* |
| Cape wildcat | *Felis lybica* |
| Cape fox | *Vulpes chama* |
| bat-eared fox | *Otocyon megalotis* |
| black-backed jackal | *Canis mesomelas* |
| aardwolf | *Proteles cristatus* |
| zorilla | *Ictonyx striatus* |
| small-spotted genet | *Genetta genetta* |
| small grey mongoose | *Galerella pulverulenta* |
| yellow mongoose | *Cynictis penicillata* |
| suricate | *Suricatta suricata* |
| water mongoose | *Atilax paludinosus* |
| **PRIMATES:** | |
| chacma baboon | *Papio ursinus* |
| vervet monkey | *Cercopithicus aethiops* |
| **SMALL MAMMALS & RODENTS** | |
| Cape porcupine | *Hystrix africaeaustralis* |
| Cape ground squirrel | *Xerus inauris* |
| springhare | *Pedetes capensis* |
| elephant shrew | *Elephantulus* spp. |

University of Pretoria etd – Davies, R A G (1994)


APPENDIX 2 cont.

| | |
|---|---|
| HYRAX: | |
| rock hyrax | *Procavia capensis* |
| LAGOMORPHS: | |
| Smith's red rock rabbit | *Pronolagus rupestris* |
| Cape hare | *Lepus capensis* |
| scrub hare | *Lepus saxatilis* |
| UNGULATES: | |
| domestic sheep | *Ovis aries* |
| domestic goat | *Capra hircus* |
| klipspringer | *Oreotragus oreotragus* |
| springbok | *Antidorcas marsupialis* |
| mountain reedbuck | *Redunca fulvorufula* |
| grey rhebok | *Pelea capreolus* |
| steenbok | *Raphicerus campestris* |
| grey duiker | *Silvicapra grimmia* |
| BIRDS: | |
| Ludwig's bustard | *Neotis ludwigii* |
| karoo horhaan | *Eupodotis vigorsii* |
| helmeted guinea fowl | *Numida meleagris* |
| greywing francolin | *Francolinus africanus* |
| Egyptian goose | *Alopochen aegyptiacus* |
| African black duck | *Anas sparsa* |
| yellow-billed duck | *Anas undulata* |
| redeyed dove | *Streptopelia semitorquata* |
| rock pigeon | *Columba guinea* |
| white-necked raven | *Corvus albicollis* |
| black-necked heron | *Ardea melanocephala* |
| black stork | *Ciconia nigra* |
| Alpine swift | *Apus melba* |
| REPTILES: | |
| rock leguaan | *Varanus exanthematicus albigularis* |
| southern rock agama | *Agama atra* |
| Cape cobra | *Naja nivea* |
| puff adder | *Bitis arietans* |
| tent tortoise | *Psammobates tentorius* |
| greater padloper | *Homopus femoralis* |
| leopard tortoise | *Geochelone pardalis* |

University of Pretoria etd – Davies, R A G (1994)


# APPENDIX 3

## BREEDING HISTORIES OF BLACK EAGLE PAIRS IN THE KRNP

| | | ANNUAL BREEDING STATUS | | | | | |
|---|---|---|---|---|---|---|---|
| PAIR | | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
| KF | Kookfontein | | S | S | N | S | |
| DH | Doringhoek | S | F1 | F1 | N | N | (N) |
| SL | Sloop | S | N | S | S | N | (N) |
| BK | Bakenkop | S | S | F2 | S | F3 | (A) |
| LH | Lion's Head | N/F | F4 | S | S | S | (A) |
| BR | Beagle Ravine | F5 | S | N | N | N | (N) |
| KK | Kortkloof | S | N | F6 | S | F5 | (A) |
| PB | Penberi | S | N | S | S | S | (A) |
| ZZ | Zig-zag Kloof | S | F7 | S | N | S | (A) |
| LF | Lemoenfontein | | N | F8 | S | S | (A) |
| TG | The Gate | | | ? | ? | | |
| GD | Gamka Dam | N/F | S | S | F9 | S | (A) |
| MP? | Molteno Pass | N/F | N | N | N | N | |
| MV | Mountain View | ? | | F2 | S | S | |
| TC | Tower Cliffs | S | N | N | N | S | |
| RC | Red Castle | N | N | N | F3 | N | |
| LC | Lancelot | ? | S | N | N | S | |
| SK | Skomer | ? | N | S | S | N | |
| WC | Weeping Cliffs | | ? | N | N | N | |
| VC | Vulture Cliffs | | ? | S | N | N | |
| PK | Paardekraal | | | S | N | | |
| CC | Corner Cliffs | | | S | N | | |
| LX | Loxton Road | S | S | S | S | S | (A) |

KEY: blank spaces represent unmonitored nests; N=not breeding; F=failed attempt; S=successful attempt; A=attempt; ? see notes.

NEST FAILURES:
F1 Galerella pulverulenta predates newly hatched chick
F2 disappearance of small chick
F3 disappearance of large chick
F4 large chick (78d old) dies of impacted crop
F5 unknown
F6 infertile egg
F7 small chick (10d old) abandoned
F8 disappearance of egg or small chick
F9 one egg disappears; remaining small chick (2d old) blown out of nest bowl

NOTES:
MV and LC probably raised chicks, and SK probably didnt breed in 1986 (insufficient data); F7 was caused by the death of resident adult male in August 1987 (drowned in resevoir), ZZ bred again 9 months later in 1988; SL nest (1 of 2) collapsed in 1987 perhaps leading to a non-breeding season; VC probably didnt breed, and WC eggs may have been lost to Corvus albicollis in 1987; juvenile found electocuted near TC eyrie in June 1987 (could have been 1986 fledgling from this site); GD female did not desert despite massive human interference (road building) during the 1988 nesting season; An adult female (possibly TC) was killed by colliding with an FM mast in July 1988, TC bred again 23 months later in 1990; TG probably raised a chick in 1988, and probably made a breeding attempt in 1989 (insufficient data); LF birds may have been shot at on their eyrie during 1989 but they raised a chick nonetheless; WC female (identifiable by white spots) was injured some time after July 1989, she displaced the DH female in 1990, but the WC male was still single for this breeding season; ZZ nest (1 of 2) collapsed in 1991; BR female replaced by new subadult in 1991; Molteno Pass pair never bred and were rarely present in territory. ME in Figure 41 refers to martial eagle.

University of Pretoria etd – Davies, R A G (1994)


# APPENDIX 4

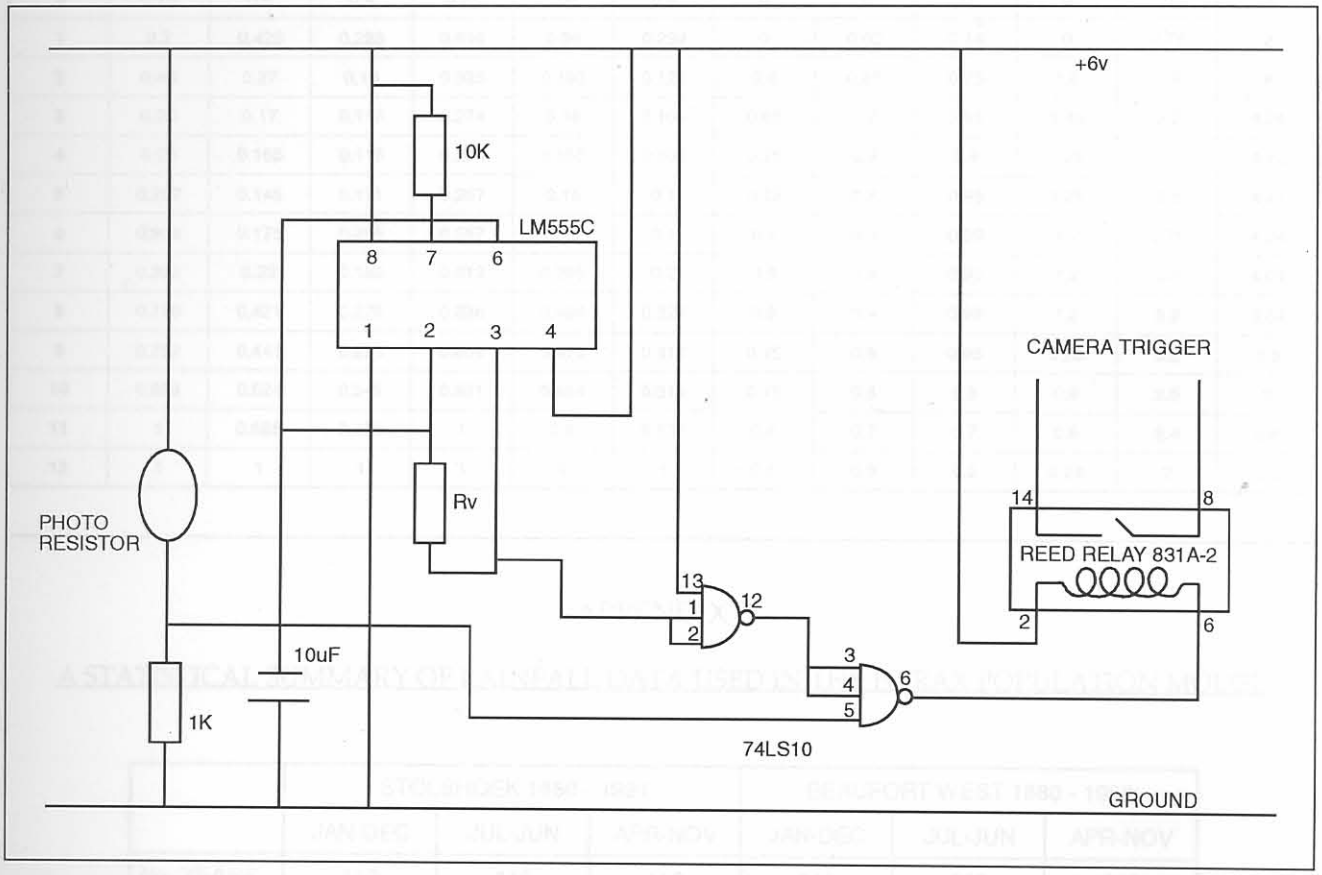
## DETAILS RECORDED FOR EACH CARACAL TRAPPED

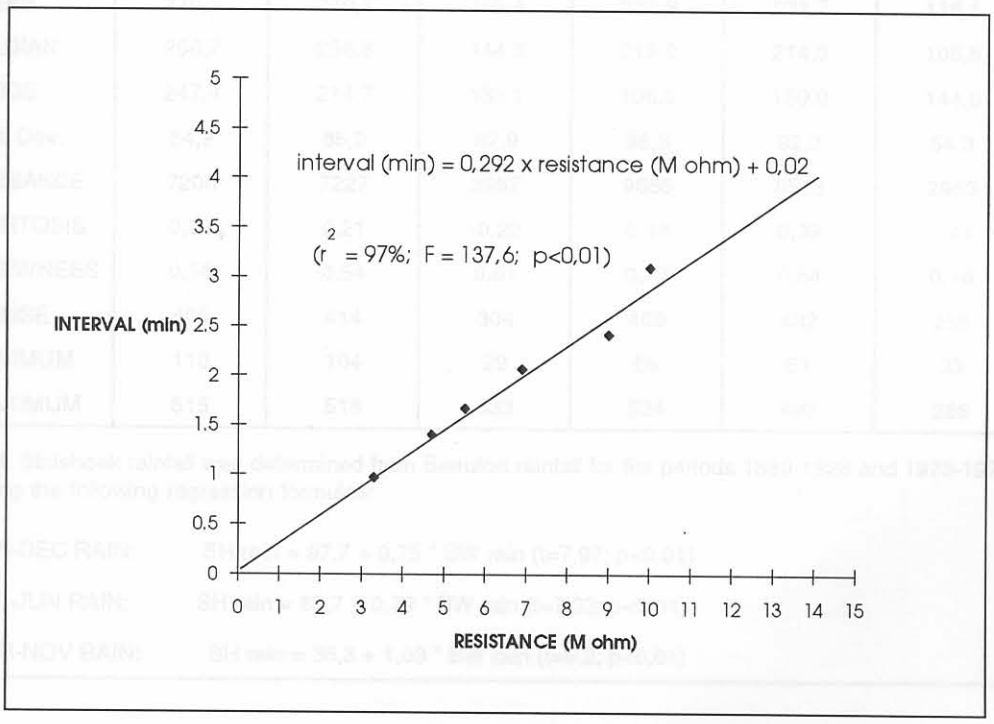
| | TANJA | ANDY | MLILO | LUKE |
|---|---|---|---|---|
| DATE | 25/1/88 | 10/4/88 | 27/4/88 | 11/5/88 |
| LOCALITY | Moordenaarsgat | south of Stolshoek | middle plateau | middle plateau |
| BAIT | none | blood, sand | blood, sand | blood, sand |
| SEX | female | female | female | male |
| MASS | 4,9kg | 5,89kg | 10,5kg | 14,8kg |
| CONDITION | fair | good | fair | fair |
| AGE? | sub-adult | sub-adult | adult | adult (4y) |
| TOTAL LENGTH | 85cm | 88cm | 111cm | 124cm |
| BODY LENGTH | 65cm | 64cm | 86cm | 91cm |
| SHOULDER HEIGHT | | 34cm | 40cm | 44cm |
| HEAD CIRCUMFERENCE | 23cm | 24cm | 28cm | 35cm |
| NECK CIRCUMFERENCE | 18cm | 18cm | 22cm | 26cm |
| COLLAR SIZE | 25cm | 23cm | 26cm | 29cm |
| ROMPUN | none | 0,8ml | 1,0ml | 1,5ml |
| KETAMINE | 125mg | 50mg | 100mg | 75mg |
| PERIOD OF ANAESTHESIA | 2h | 2h | 1h 50min | 2h 20min |
| RADIO-COLLAR | B2C9 | B1C7 | B1C9 | B1C5 |

University of Pretoria etd – Davies, R A G (1994)

# APPENDIX 5
## CIRCUIT DIAGRAM FOR THE TIME-LAPSE SYSTEM AND A PLOT OF THE REGRESSION OF TIME INTERVAL ON VARIABLE RESISTANCE

The circuit was compiled by K. Musgrave (Diginet Systems, Pretoria) after Temple (1972). Part numbers are provided. Rv denotes the variable resistor that could be altered to adjust the time interval (see regression below).



University of Pretoria etd – Davies, R A G (1994)


# APPENDIX 6

## AGE-SPECIFIC FECUNDITY AND MORTALITY DATA USED IN THE HYRAX POPULATION MODEL

| AGE CLASS | MALE MORTALITY RATES | | | FEMALE MORTALITY RATES | | | PREGNANCY RATES | | | LITTER SIZES | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BAD | AVERAGE | GOOD | BAD | AVERAGE | GOOD | BAD | AVERAGE | GOOD | BAD | AVERAGE | GOOD |
| 0 | 0.75 | 0.6 | 0.4 | 0.75 | 0.6 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 | 0.7 | 0.425 | 0.283 | 0.616 | 0.36 | 0.239 | 0 | 0.02 | 0.14 | 0 | 0.75 | 2 |
| 2 | 0.46 | 0.27 | 0.18 | 0.325 | 0.193 | 0.126 | 0.6 | 0.65 | 0.75 | 1.6 | 1.8 | 4 |
| 3 | 0.29 | 0.17 | 0.113 | 0.274 | 0.16 | 0.106 | 0.65 | 0.7 | 0.85 | 1.48 | 2.2 | 4.24 |
| 4 | 0.29 | 0.165 | 0.113 | 0.274 | 0.155 | 0.106 | 0.75 | 0.8 | 0.9 | 1.28 | 2.25 | 4.22 |
| 5 | 0.257 | 0.145 | 0.171 | 0.257 | 0.15 | 0.1 | 0.75 | 0.8 | 0.95 | 1.28 | 2.5 | 4.21 |
| 6 | 0.308 | 0.175 | 0.205 | 0.257 | 0.15 | 0.1 | 0.8 | 0.9 | 0.99 | 1.2 | 2.75 | 4.04 |
| 7 | 0.393 | 0.23 | 0.153 | 0.513 | 0.295 | 0.2 | 0.8 | 0.9 | 0.99 | 1.2 | 3.2 | 4.04 |
| 8 | 0.718 | 0.421 | 0.279 | 0.838 | 0.494 | 0.326 | 0.8 | 0.9 | 0.99 | 1.2 | 3.2 | 3.64 |
| 9 | 0.752 | 0.441 | 0.293 | 0.804 | 0.473 | 0.313 | 0.75 | 0.8 | 0.95 | 1.28 | 3.2 | 3.3 |
| 10 | 0.889 | 0.524 | 0.346 | 0.821 | 0.484 | 0.319 | 0.75 | 0.8 | 0.8 | 0.8 | 2.5 | 3 |
| 11 | 1 | 0.685 | 0.452 | 1 | 0.8 | 0.532 | 0.6 | 0.7 | 0.7 | 0.8 | 2.4 | 2.6 |
| 12 | 1 | 1 | 1 | 1 | 1 | 1 | 0.5 | 0.6 | 0.6 | 0.24 | 2 | 2.5 |

# APPENDIX 7

## A STATISTICAL SUMMARY OF RAINFALL DATA USED IN THE HYRAX POPULATION MODEL

| | STOLSHOEK 1880 - 1991 | | | BEAUFORT WEST 1880 - 1989 | | |
|---|---|---|---|---|---|---|
| | JAN-DEC | JUL-JUN | APR-NOV | JAN-DEC | JUL-JUN | APR-NOV |
| No. YEARS | 112 | 112 | 112 | 110 | 110 | 110 |
| MEAN | 270,3 | 270,2 | 155,4 | 232,9 | 231,7 | 116,1 |
| MEDIAN | 256,7 | 258,8 | 144,5 | 212,0 | 214,0 | 105,5 |
| MODE | 247,4 | 214,7 | 133,1 | 106,0 | 159,0 | 144,0 |
| Std. Dev. | 84,9 | 85,0 | 62,9 | 98,3 | 92,3 | 54,3 |
| VARIANCE | 7206 | 7227 | 3957 | 9665 | 8513 | 2953 |
| KURTOSIS | 0,33 | 0,21 | -0,22 | 0,43 | 0,39 | 0,41 |
| SKEWNESS | 0,58 | 0,54 | 0,61 | 0,77 | 0,84 | 0,76 |
| RANGE | 405 | 414 | 304 | 469 | 432 | 255 |
| MINIMUM | 110 | 104 | 29 | 65 | 61 | 33 |
| MAXIMUM | 515 | 518 | 333 | 534 | 493 | 288 |

N.B. Stolshoek rainfall was determined from Beaufort rainfall for the periods 1880-1928 and 1973-1977 using the following regression formulae:

JAN-DEC RAIN: SH rain = 97,7 + 0,75 * BW rain (t=7,97; p<0,01)

JUL-JUN RAIN: SH rain = 89,7 + 0,79 * BW rain (t=7,33; p<0,01)

APR-NOV RAIN: SH rain = 36,3 + 1,03 * BW rain (t=9,2; p<0,01)

University of Pretoria etd - Davies, R A G (1994)


# APPENDIX 8

## PREFERENCE RATINGS FOR SELECTION OF HYRAX AGE-CLASSES BY BLACK EAGLES

These were calculated as %use/%availability after Petrides (1975) - see Chapter 10

| AGE CLASS | PREFERENCE RATINGS | |
|---|---|---|
| | MALES | FEMALES |
| 0 | 0.393 | 0.392 |
| 1 | 1.801 | 1.297 |
| 2 | 1.175 | 0.907 |
| 3 | 0.941 | 1.072 |
| 4 | 1.134 | 0.916 |
| 5 | 0.817 | 0.913 |
| 6 | 1.082 | 0.922 |
| 7 | 1.447 | 2.035 |
| 8 | 1.763 | 3.309 |
| 9 | 1.453 | 3.000 |
| 10 | 2.972 | 2.191 |
| 11 | 2.732 | 4.869 |
| 12 | 3.932 | 4.068 |

# APPENDIX 9

## AGE-SPECIFIC DATA ON 'NON-EAGLE' MORTALITY USED IN THE HYRAX POPULATION MODEL

| AGE CLASS | MORTALITY RATES TO FACTORS OTHER THAN EAGLES | | | | | |
|---|---|---|---|---|---|---|
| | MALES | | | FEMALES | | |
| | BAD | AVERAGE | GOOD | BAD | AVERAGE | GOOD |
| 0 | 0.701 | 0.561 | 0.374 | 0.700 | 0.561 | 0.374 |
| 1 | 0.383 | 0.224 | 0.149 | 0.355 | 0.216 | 0.144 |
| 2 | 0.234 | 0.139 | 0.091 | 0.156 | 0.092 | 0.061 |
| 3 | 0.11 | 0.064 | 0.042 | 0.066 | 0.039 | 0.026 |
| 4 | 0.065 | 0.037 | 0.025 | 0.091 | 0.052 | 0.036 |
| 5 | 0.087 | 0.051 | 0.034 | 0.083 | 0.047 | 0.047 |
| 6 | 0.087 | 0.051 | 0.034 | 0.081 | 0.046 | 0.046 |
| 7 | 0.117 | 0.067 | 0.045 | 0.113 | 0.066 | 0.044 |
| 8 | 0.38 | 0.224 | 0.148 | 0.208 | 0.112 | 0.081 |
| 9 | 0.476 | 0.28 | 0.185 | 0.232 | 0.136 | 0.084 |
| 10 | 0.322 | 0.19 | 0.125 | 0.405 | 0.239 | 0.158 |
| 11 | 0.475 | 0.38 | 0.225 | 0.369 | 0.253 | 0.167 |
| 12 | 0.551 | 0.551 | 0.551 | 0.518 | 0.518 | 0.518 |

University of Pretoria etd – Davies, R A G (1994)



# APPENDIX 10

## HYRAX POPULATION MODEL (TURBO PASCALL version 7.0 Borland International Inc.)

*{all comments italicised and enclosed in {} are not read by the program}*

```
program hyrax(input,output);
USES CRT;
CONST   FETAL_RESORPTION = 0.11;                    { foetal resorption rate }
        RESORPTION_GOODyr = 0.02;                   { same for good years }
        RESORPTION_BADyr = 0.2;                     { same for bad years  }
        WINTER_CAPITAL = 126994;                    { 14.7% of winter capital under standard conditions }
        CAPITAL_CONSTRAINT = 0.3;                   { proportion of capital which can be depleted or gained }
        INTEREST_RATE = 0.37267;                    { fresh growth during standard year, as the proportion of standard capital }
        HYRAX_FOOD_CONSUMPTION = 26.061;            { Kg/hyrax/yr }
        STD_KC = 1816;                              { K under standard conditions }
        EDIBILITY = 0.1;                            { proportion of winter capital edible }
        SHEEP_EQUIV = 10;                           { metabolic equivalent of one adult sheep in hyrax}
        COST_PER_SHEEP = 30;                        { cost of letting veld per sheep per year in Rands}

TYPE    age_array  = ARRAY[0..12] of REAL;
        year_array = ARRAY[1870..1995] of INTEGER;

VAR     M_prev,M_next,F_prev,F_next,Fecundity,Fec_bd, Fec_av,Fec_gd:        age_array;
        incmort_F,incmort_F_bd,incmort_F_av,incmort_F_gd,othmort_F:         age_array;
        othmort_F_bd,othmort_F_av,othmort_F_gd,incmort_M,incmort_M_bd:      age_array;
        incmort_M_av,incmort_M_gd,othmort_M,othmort_M_bd,othmort_M_av:      age_array;
        othmort_M_gd,actmort_F,actmort_M,actdie_F,actdie_M,incdie_F:        age_array;
        incdie_M,othdie_F,othdie_M,Pregnancy,Preg_bd,Preg_av,Preg_gd:       age_array;
        LitterSize,Litr_bd,Litr_av,Litr_gd,F_die, M_die, Pref_M, Pref_F:    age_array;
        F_tmp,M_tmp,M_eagle_kill,F_eagle_kill,M_lynx_kill,F_lynx_kill:      age_array;
        summer_rain,gestn_rain,gestn_rain_SH,summer_rain_SH:                year_array;
        gestn_rain_BW, summer_rain_BW:                                      year_array;
        mean_summer_rain, min_summer_rain, max_summer_rain:                 REAL;
        mean_gestn_rain, min_gestn_rain, max_gestn_rain:                    REAL;
        mean_gestn_rain_SH,mean_gestn_rain_BW,max_gestn_rain_SH:            REAL;
        max_gestn_rain_BW,min_gestn_rain_SH,min_gestn_rain_BW:              REAL;
        mean_summer_rain_SH,mean_summer_rain_BW,max_summer_rain_SH:         REAL;
        max_summer_rain_BW,min_summer_rain_SH,min_summer_rain_BW:           REAL;
        No_Hyrax_prev,No_Hyrax_next, r, No_males, No_Females, No_babies :   REAL;
        K_prev,SR,fjuv,fimm,f2yr,fads,fold,KC,std_resource,std_growth:      REAL;
        resorption,K_ratio,P_ratio,K_factor,crash_level,crash_mort:         REAL;
        capital,food_eaten,food_resource,fresh_growth:                      REAL;
        fresh_growth_1,prop_growth_eaten,Prod_mult,foet_mult:               REAL;
        min_mult,max_mult,unpal_buffer,start_pop,sheep,cost:                REAL;
        correction,Sum_C,prey_availability,eagle_kill,Comp_Old:             REAL;
        R_diff,total_rain_SH,total_rain_BW,impede,version:                  REAL;
        alt_demand,eagle_alt,lynx_alt,Diff_K,No_HP,Surplus,Lynx_increase:   REAL;
        Lynx_Decline,Lynx_Diet_Min,Lynx_Diet_Max,Lynx_Consumption:          REAL;
        Dassie_Meat,lynx_mult,Lynx_Nos,Lynx_Prev,Lynx_Food,Surplus_Per_Lynx: REAL;
        Lynx_Diet,lynx_kill,total_dying,other_dying,pop_growth,juv_loss:    REAL;
        rec_loss,loss_above,loss_below,mort_above,mort_below:               REAL;
        no_crashes:                                                         INTEGER;
        year,i,y,generation,first_date,last_date,start_date,end_date:       INTEGER;
        rain_locality,yn:                                                   CHAR;
        remove_eagle_effect,age_selection,terminate_model,bias:             BOOLEAN;
        Demogr_file,Rain_file,outmain_out,outagest_out,outagepr_out:        TEXT;

procedure eagle_predation; forward;
procedure lynx_predation; forward;

{ ********************************************************************************************************
  ************************************** P R O C E D U R E S **************************************
  ********************************************************************************************************}
procedure read_rainfall;
{
=========================================================================================
        R A I N F A L L   S U B - R O U T I N E
        Read in the rainfall data (1878-1989): calculate maximum, minimum and mean values; initialise gestn_rain and summer_rain variables.
=========================================================================================
}
VAR Rain_file:TEXT;
  no_years,y:INTEGER;
BEGIN
Assign(Rain_file,rain_locality+'_RAIN.DAT');
reset(Rain_file);
mean_gestn_rain := 0;                               { Initialise accumulators, maxima & minima }
mean_summer_rain := 0;
Min_gestn_rain := 10000;
Max_gestn_rain := 0;
Max_summer_rain := 0;
Min_summer_rain := 10000;
no_years := 0;
readln(Rain_file);                                  { Read file heading with captions }
read(Rain_file,year,summer_rain[year],gestn_rain[year]);
first_date := year;                                 { Determine 1st rainfall year }
repeat
        read(Rain_file,year,summer_rain[year],gestn_rain[year]);   { Read rainfall figures }
        if gestn_rain[year] < Min_gestn_rain then Min_gestn_rain := gestn_rain[year];
```

University of Pretoria etd – Davies, R A G (1994)


```
            if gestn_rain[year] > Max_gestn_rain then Max_gestn_rain := gestn_rain[year];        {calculating maxima and minima .... }
            if summer_rain[year] < Min_summer_rain then Min_summer_rain := summer_rain[year];
            if summer_rain[year] > Max_summer_rain then Max_summer_rain := summer_rain[year];
            mean_gestn_rain := mean_gestn_rain + gestn_rain[year];
            mean_summer_rain := mean_summer_rain + summer_rain[year];
            inc(no_years);
until eof(Rain_file)=TRUE;
last_date := year;                                                   { Determine last rainfall year }
mean_gestn_rain := mean_gestn_rain/no_years;                         { Calculate mean values }
mean_summer_rain := mean_summer_rain/no_years;
close(Rain_file);
END;

procedure vegetation_grow(Year:INTEGER; No_Dassies: REAL);
{
=============================================================================================
                        LOWER TROPHIC (VEGETATION) LEVEL
        This procedure takes winter phytomass from the previous year and calculates fresh growth in accordance with summer rainfall
        phytomass subsequently accumulates or slightly declines in accordance with rainfall
        If fresh growth is not sufficient to meet hyrax food demands, the deficit is removed from the phytomass.
=============================================================================================
}
VAR consumption_ratio,rain_mult:REAL;
BEGIN
 rain_mult := min_mult + (max_mult-min_mult) * (summer_rain[Year-1]-min_summer_rain)/(max_summer_rain-min_summer_rain);
 capital := capital * rain_mult;                                     {modify phytomass according to rain}
 food_eaten := No_Dassies * DASSIE_FOOD_CONSUMPTION;
 consumption_ratio := food_eaten/fresh_growth;
 if consumption_ratio > 1 then
   capital := capital - (1-unpal_buffer)*(food_eaten - fresh_growth);  {depletion of phytomass by heavy grazing}
 if capital > WINTER_CAPITAL*(1+CAPITAL_CONSTRAINT) then              { Limit the annual change in capital }
            capital := WINTER_CAPITAL*(1+CAPITAL_CONSTRAINT);
 if capital < WINTER_CAPITAL*(1-CAPITAL_CONSTRAINT) then
            capital := WINTER_CAPITAL*(1-CAPITAL_CONSTRAINT);
 prod_mult := 1 + (1.5 * (summer_rain[Year]-mean_summer_rain)/mean_summer_rain);   { Calculate fresh growth: }
 if prod_mult < 0.05 then prod_mult := 0.05;
 fresh_growth_1 := fresh_growth;
 fresh_growth := prod_mult * INTEREST_RATE * capital;
 food_resource := edibility * capital + fresh_growth;                { Calculate K = food supplies around rocks}
 std_resource := interest_rate * winter_capital + edibility * winter_capital;
 KC := std_KC * food_resource/std_resource;
END;

procedure dassie_reproduce(year:INTEGER;K:REAL);
{
=============================================================================================
                        HYRAX LEVEL
        This procedure models the events in the hyrax population. Carrying capacity is used to determine the age-specific
        mortality and fecundity rates.. Age-specific predation is also included here
=============================================================================================
}
VAR upper_range, lower_range :REAL;
BEGIN
 K_ratio := No_Hyrax_prev/K_prev;                                    { Ratio: (current_#_dassies)/(prev. years' carrying capacity) }
 Diff_K := Abs(K_prev-No_Hyrax_prev);
 P_ratio := K_ratio;                                                 { remove ratio at this stage}
 if K_ratio > K_factor then K_ratio := K_factor                      { compare ratio with level at which max/min mortality rates set in}
 else if K_ratio < (1/K_factor) then K_ratio := 1/K_factor;
 If K_ratio >= 1 then                                                { Scale K_ratio }
    K_ratio := 0 - (K_ratio - 1)/(K_factor - 1)
 else
    K_ratio := (1 - K_ratio) / (1 - (1/K_factor));
 for i:=0 to 12 do begin                                             { For each hyrax age class: }
    incmort_F[i] := incmort_F_av[i] - K_ratio * (incmort_F_av[i]-incmort_F_gd[i]);   { calculate age-specific mortalities, }
    incmort_M[i] := incmort_M_av[i] - K_ratio * (incmort_M_av[i]-incmort_M_gd[i]);
    othmort_F[i] := othmort_F_av[i] - K_ratio * (othmort_F_av[i]-othmort_F_gd[i]);
    othmort_M[i] := othmort_M_av[i] - K_ratio * (othmort_M_av[i]-othmort_M_gd[i]);
    Pregnancy[i]  := Preg_av[i] + K_ratio * (Preg_gd[i]-Preg_av[i]);  { age-specific pregnancy rate, }
    LitterSize[i] := Litr_av[i] + K_ratio * (Litr_gd[i]-Litr_av[i]);  { age-specific litter size, }
    incdie_F[i] := incmort_F[i] * F_prev[i];                         { total number of female hyrax dying }
    othdie_F[i] := othmort_F[i] * F_prev[i];                         { non-eagle mortality }
    incdie_M[i] := incmort_M[i] * M_prev[i];                         { (-M-suffix = MALE; -F = FEMALE) }
    othdie_M[i] := othmort_M[i] * M_prev[i];
 end;
 R_diff := gestn_rain[year]-mean_gestn_rain;                         { Assess gestation rainfall }
 upper_range := max_gestn_rain - mean_gestn_rain;
 lower_range := mean_gestn_rain - min_gestn_rain;
 if R_diff >= 0 then                                                 { calculate foetal resorption in Good year: }
    resorption := FETAL_RESORPTION - (R_diff/upper_range) * (FETAL_RESORPTION - RESORPTION_GOODyr)
 else                                                                { In Bad year: }
    resorption := FETAL_RESORPTION + (R_diff/lower_range) * (RESORPTION_BADyr - FETAL_RESORPTION);
 foet_mult := gestn_rain[year]/mean_gestn_rain;
 if foet_mult > 1.4 then foet_mult := 1.4;
 if foet_mult < 0.6 then foet_mult := 0.6;
 eagle_predation;                                                    { call in eagle predation here }
 lynx_predation;                                                     {  call in caracal predation here }
 alt_demand := eagle_alt + lynx_alt;                                 { calculate predator demand for alternate prey }
```

University of Pretoria etd – Davies, R A G (1994)


```
{ ------------------------------------------------------------
        TO DECIDE ON FINAL MORTALITY RATE DEPENDING ON PREDATOR REMOVAL ETC.
    Choose model version    1. inclusive motality
                            2. separate (remove?) eagle mortality from other mortality
                            3. impede predators
  ------------------------------------------------------------ }
 if version = 1 then
   for i:=0 to 12 do begin
    actmort_M[i] := incmort_M[i];                          { all mortality modelled inclusively }
    actmort_F[i] := incmort_F[i];
   end;
 if version = 2 then
  for i:=0 to 12 do begin
    if remove_eagle_effect = FALSE then begin
      actmort_M[i] := M_eagle_kill[i]/M_prev[i] + othmort_M[i];   { model eagle mortality and other mortality separately }
      actmort_F[i] := F_eagle_kill[i]/F_prev[i] + othmort_F[i];
      end
    else begin                                             { remove eagles  - captured hyrax do not die }
      actmort_M[i] := othmort_M[i] + Comp_old*M_eagle_kill[i]/M_prev[i];   { except for a small portion dying of old age etc. }
      actmort_F[i] := othmort_F[i] + Comp_old*F_eagle_kill[i]/F_prev[i];
      end
  end;
  if version = 3 then
  for i:=0 to 12 do begin                                  { both predators impeded by X% - }
     actdie_M[i] := ((1-impede) * M_eagle_kill[i]) +  (othdie_M[i] - (impede * M_lynx_kill[i]));   { X% of would be kills do not die }
     actmort_M[i] := actdie_M[i]/M_prev[i];
     actdie_F[i] := ((1-impede) * F_eagle_kill[i]) +  (othdie_F[i] - (impede * F_lynx_kill[i]));
     actmort_F[i] := actdie_F[i]/F_prev[i];
  end;

{========== ALL MODEL VERSIONS : ==========}

 if P_ratio > crash_level then begin                       { Heavy compensatory mortality due to starvation / disease .. }
    inc(no_crashes);                                       { when P far exceeds K }
    for i:= 0 to 12 do begin
          actmort_F[i] :=  crash_mort;
          actmort_M[i] :=  crash_mort;
          end;
    end;
 no_babies := 0;                                           { Accumulate populations statistics: }
 No_Females := 0;                                          { initialise accumulators }
 No_Males := 0;
 No_Hyrax_next := 0;
 total_dying := 0;
 for i:=1 to 12 do begin
     M_next[i] := M_prev[i-1] * (1-actmort_M[i-1]);        { Implement mortality rates that were decided upon above }
     F_next[i] := F_prev[i-1] * (1-actmort_F[i-1]);
     No_babies := No_babies + F_next[i] * Pregnancy[i] * LitterSize[i] * (1 - resorption);
     No_Females := No_Females + F_next[i];
     No_Males := No_Males + M_next[i];
     No_Hyrax_next := No_Hyrax_Next + F_next[i] + M_next[i];
     total_dying := total_dying + M_prev[i-1]*actmort_M[i-1] + F_prev[i-1]*actmort_F[i-1];
     end;
 total_dying := total_dying + M_prev[12] + F_prev[12];
 other_dying := total_dying - eagle_kill;
 if bias = TRUE then                                       { If selected, implement rainfall bias in sex ratio of juveniles }
   F_next[0] := (No_babies/2)*foet_mult                    {    using modifiers calculated for foetal resorption earlier     }
 else
   F_next[0] := No_babies/2;
 M_next[0] := No_babies-F_next[0];
 No_Hyrax_next := No_Hyrax_Next + No_babies;

 pop_growth := (No_Hyrax_next-No_Hyrax_Prev)/No_Hyrax_Prev;
 rec_loss := (2.345*No_Females)-No_babies;                 { measure losses through the upper and lower trophic levels }
 juv_loss := (M_prev[0]-M_next[1]) + (F_prev[0]-F_next[1]);
 loss_above := (eagle_kill + lynx_kill + (0.2*juv_loss));  { # hyrax dying from predation  }
 loss_below := rec_loss + (total_dying-loss_above);        { # hyrax dying from starvation etc. }
 mort_above := loss_above/No_Hyrax_Prev;
 mort_below := loss_below/No_Hyrax_Prev;

 No_Females := No_Females + F_next[0];
 No_Males := No_Males + F_next[0];
 r := ln(No_Hyrax_next/No_Hyrax_prev);
 SR := (No_Females-F_next[0]-F_next[1])/(No_Males-M_next[0]-M_next[1]);   { Calculate sex ratio }
 fjuv := (F_next[0]+M_next[0])/No_Hyrax_next;              { Calculate  population composition }
 fimm := (F_next[1]+M_next[1])/No_Hyrax_next;
 f2yr := (F_next[2]+M_next[2])/No_Hyrax_next;
 fads := (F_next[3]+M_next[3]+F_next[4]+M_next[4]+F_next[5]+M_next[5]
      +F_next[6]+M_next[6]+F_next[7]+M_next[7])/No_Hyrax_next;
 fold := (F_next[8]+M_next[8]+F_next[9]+M_next[9]+F_next[10]+M_next[10]
       +F_next[11]+M_next[11]+F_next[12]+M_next[12])/No_Hyrax_next;
 for i:=0 to 12 do begin                                   { Age-specific values for next generation become current }
     F_prev[i] := F_next[i];
     M_prev[i] := M_next[i];
     No_Hyrax_prev := No_Hyrax_next;
     end;
 K_prev := K;
END;
```

University of Pretoria etd – Davies, R A G (1994)


```
procedure eagle_predation;
{
=============================================================================
                    CALCULATE LOSSES TO EAGLES:
=============================================================================
}
BEGIN
No_HP := No_Hyrax_prev;
if No_HP > 2*std_KC then No_HP :=2*std_KC;                    { temporary constraints on the number of hyrax available }
if No_HP < 1200 then No_HP := 1200;
if No_HP > std_KC then eagle_kill := 175 + 175*(No_HP - std_KC)/std_KC    { calculate number captured in direct relation to abundance }
          else eagle_kill := 175 - 105*(std_KC - No_HP)/1200;            {   (at low abundance)  }
prey_availability := P_ratio;
if prey_availability > 1.4 then prey_availability := 1.4;     { P:K ratio is used here as an indication of hyrax 'availability' }
if prey_availability < 0.6 then prey_availability := 0.6;
eagle_kill := eagle_kill * prey_availability;                 { Modify number taken according to hyrax availability }
if eagle_kill > 350 then eagle_kill := 350;
if eagle_kill < 70 then eagle_kill := 70;                     { constrain the hyrax kill by eagles within indicated limits}
eagle_alt := 220-eagle_kill;                                  { eagle demand for alternate prey }
if eagle_alt < 0 then eagle_alt := 0;

if age_selection = FALSE then                                 { for test-runs of the model assuming no age-selection of hyrax }
   for i:=0 to 12 do begin
      Pref_M[i] := 1;
      Pref_F[i] := 1;
      end;
Sum_C := 0;
for i:=0 to 12 do begin
   M_tmp[i] := M_prev[i] * Pref_M[i];                         { create 'artificial' availability accoding to eagle preferences }
   F_tmp[i] := F_prev[i] * Pref_F[i];
   sum_C := sum_C + F_tmp[i] + M_tmp[i];
   end;
correction := eagle_kill / sum_C;
 for i:=0 to 12 do begin                                      {  calculate age-specific predation by eagles by   }
   M_eagle_kill[i] := M_tmp[i] * correction;                  {  'reducing' the artificial composition to conform to the # taken }
   F_eagle_kill[i] := F_tmp[i] * correction;
   end;
END;

procedure lynx_predation;
{
=============================================================================
                    CALCULATE LOSSES TO  CARACALS
=============================================================================
}
VAR rainfall_mult, min_growth, max_growth: REAL;
BEGIN
 Surplus := No_Hyrax_prev - K_prev - (0.75*eagle_kill);       { caracal diet is modelled on this hyrax 'surplus'  }
 if Surplus < 0 then Surplus := 0;                                    { but eagles are allowed to remove most of their kill first }
 Lynx_Increase := 1.4;                                        { Set bounds to rate of change in caracal numbers }
 Lynx_Decline  := 0.55;
 Lynx_Diet_Min := 0.02;                                       { Set bounds to caracal functional response (% hyrax in diet) }
 Lynx_Diet_Max := 0.50;
 Lynx_Consumption := 463;                                     {kg/caracal/yr}
 Dassie_Meat := 1.122;                                        {kg meat on average hyrax}

 Min_Growth :=0;                                              { fresh growth is used as an indicator of environmental enrichment  ... }
 rainfall_mult := 1 + (1.5 * (max_summer_rain - mean_summer_rain)/mean_summer_rain);    { to model the caracal numeric response }
 Max_Growth := WINTER_CAPITAL*(1+CAPITAL_CONSTRAINT) * INTEREST_RATE * rainfall_mult;
 lynx_mult := Lynx_Decline + (Lynx_Increase-Lynx_Decline) *
    (Fresh_Growth_1-Min_Growth)/(Max_Growth-Min_Growth);
 Lynx_Nos := Lynx_Prev * lynx_mult;                           { derive no. of caracals in eagle territory }
 if Lynx_Nos > 7.44 then Lynx_Nos := 7.44;                    { Limit the no. of caracals }
 if Lynx_Nos < 2.39 then Lynx_Nos := 2.39;

 Lynx_Food := Lynx_Nos * Lynx_Consumption;                    { total food consumption by caracals }

 Surplus_Per_Lynx := Surplus / Lynx_Nos;                      { derive the number of surplus hyrax per caracal }
 if Surplus_Per_Lynx > 210 then Lynx_Diet := Lynx_Diet_Max     {  calculate caracal diet according to this surplus }
 else Lynx_Diet := Lynx_Diet_Min + (Lynx_Diet_Max-Lynx_Diet_Min) * (Surplus_Per_Lynx/210);
 Lynx_alt := (1-Lynx_Diet)*(Lynx_Food/Dassie_Meat);           { caracal demand for alternate prey }
 lynx_kill := (Lynx_Diet * Lynx_Food) / Dassie_Meat;          { No. of hyrax killed by caracals }

Surplus := Surplus + (0.75*eagle_kill);                       { estimation of the cost of hyrax surpluses in terms of sheep grazing }
 sheep := Surplus/SHEEP_EQUIV;
 cost := sheep * COST_PER_SHEEP;

 for i:=0 to 12 do begin
   M_lynx_kill[i] := M_prev[i]/No_hyrax_prev * lynx_kill;     {  hyrax kill by caracals is calculated  ...  }
   F_lynx_kill[i] := F_prev[i]/No_hyrax_prev * lynx_kill;                { assuming non-selective predation }
   if M_lynx_kill[i] > othdie_M[i] then M_lynx_kill[i] := othdie_M[i];    {   constrain caracal kill to less than non-eagle mortality }
   if F_lynx_kill[i] > othdie_F[i] then F_lynx_kill[i] := othdie_F[i];
   end;

END;
```

```
{ ************************************************************************************************
  ********************************** MAIN ROUTINE ***********************************
  ************************************************************************************************ }
begin
ClrScr;
writeln('DASSIE SIMULATION');
writeln;
write('Location (S/B/D/M). . . . . . . . . . . . . . . . . ? ');          { Read all the program parameters    }
readln(rain_locality);                                                    { which are typed in by the operator. }
rain_locality := UpCase(rain_locality);
write('Start Date  . . . . . . . . . . . . . . . . . . . ? ');
readln(start_date);
write('End Date  . . . . . . . . . . . . . . . . . . . . ? ');
readln(end_date);
write('Population size at start . . . . . . . . . . . . . ? ');
readln(Start_Pop);
if Start_Pop = Std_KC then Start_Pop := 0;
write('Deviation of P from K for max mort. rates etc. . . . ? ');
readln(K_factor);
write('Deviation of P from K for crash  . . . . . . . . . . ? ');
readln(crash_level);
write('Crash mortality rate  . . . . . . . . . . . . . . . ? ');
readln(crash_mort);
write('Phytomass increment factor in wettest years . . . . . ? ');
readln(max_mult);
write('Phytomass decline factor in driest years  . . . . . . ? ');
readln(min_mult);
write('More male babies in dry years ? (Y/N) . . . . . . . . ? ');
  readln(yn);
  yn := UpCase(yn);
  if yn = 'Y' then bias := TRUE
      else bias := FALSE;
write('Proportion hyrax food needs from less palatables  . . ? ');
readln(unpal_buffer);
writeln('Model version?  1. inclusive mortality');
writeln('                2. separate (remove?) eagle mortality');
writeln('                3. impede predators');
write('                                  . . . . . . . ? ');
readln(version);
if version = 2 then begin
write('Age-selective predation ? (Y/N) . . . . . . . . . . . ? ');
  readln(yn);
  yn := UpCase(yn);
  if yn = 'Y' then age_selection := TRUE
      else age_selection := FALSE;
write('Actually remove eagles ? (Y/N)  . . . . . . . . . . . ? ');
readln(yn);
yn := UpCase(yn);
if yn = 'Y' then remove_eagle_effect := TRUE
      else remove_eagle_effect := FALSE;
if remove_eagle_effect = TRUE then begin
  write('Compensatory mortality for old age etc. . . . . ? ');
  readln(Comp_Old);
  end;
end;
if version = 3 then begin
write('Predator impedence factor . . . . . . . . . . . . . ? ');
readln(impede);
end;
writeln;
write('Running ... ');


{ ============================================
        SECTION 1: Read in the demographic parameters:
  ============================================ }

Assign(Demogr_file,'demog.dat');                                          { Read demographic data input file: }
reset(Demogr_file);
readln(Demogr_file);                                                      { Read file heading with captions }
for i:=0 to 12 do begin                                                   { for each age class [i] }
  Readln(Demogr_file, generation,
      M_prev[i],  F_prev[i],                                              { # hyrax to begin with }
      Pref_M[i], Pref_F[i],                                               { eagle preference index }
      incmort_M_bd[i],incmort_M_av[i],incmort_M_gd[i],
      incmort_F_bd[i],incmort_F_av[i],incmort_F_gd[i],
      Preg_bd[i] ,Preg_av[i], Preg_gd[i],                                 { pregnacy (bad_year, average_year,good_year) }
      Litr_bd[i], Litr_av[i], Litr_gd[i],                                 { Litter size       ditto          }
      othmort_M_bd[i],othmort_M_av[i],othmort_M_gd[i],                    { non-eagle mortality rates }
      othmort_F_bd[i],othmort_F_av[i],othmort_F_gd[i]);
  end;
close(Demogr_file);
```

University of Pretoria etd – Davies, R A G (1994)


```
if Start_Pop <> 0 then
   for i:= 0 to 12 do begin
      M_prev[i] := Start_Pop * M_Prev[i]/Std_KC;                    { Derive hyrax population structure at start }
      F_prev[i] := Start_Pop * F_Prev[i]/Std_KC;
      end;

read_rainfall;                                                      { Read the rainfall data from the rainfall file }

assign(outmain_out,'outmain.OUT');                                  { Initialise output files and initial values: }
rewrite(outmain_out);
assign(outagest_out,'outagest.OUT');
rewrite(outagest_out);
assign(outagepr_out,'outagepr.OUT');
rewrite(outagepr_out);
capital := 165092;
fresh_growth := winter_capital * interest_rate;
No_Hyrax_prev := std_KC;
No_Hyrax_next := std_KC;
K_prev := std_KC;
Lynx_Prev := Lynx_Avg;

terminate_model := FALSE;
year := start_date - 1;
repeat                                                              { Execute the model year-by-year and write results to the output files: }
   year := year + 1;
   vegetation_grow(year,No_Hyrax_Prev);                             { This determines KC, the carrying capacity }
   if capital < 0  then terminate_model := TRUE;
   write(outmain_out,year:4,summer_rain[year]:6,gestn_rain[year]:6,capital:13:0,fresh_growth:12:0,KC:11:1);

   dassie_reproduce(year,KC);                                       { This is where most of the demographic action takes place }
   writeln(outmain_out,No_Hyrax_prev:11:1,r:9:4,total_dying:12:0,eagle_kill:8:1,Lynx_Nos:5:2,Surplus:6:0,
     lynx_kill:6:0,No_babies:5:0,other_dying:8:0,sheep:9:1,cost:10:2,pop_growth:8:4,mort_below:8:4,mort_above:8:4,
     Diff_K:10:1,no_crashes:5);
   write(outagepr_out,year:4,F_eagle_kill[0]:9:1,F_eagle_kill[1]:9:1,F_eagle_kill[2]:9:1,F_eagle_kill[3]:9:1,
     F_eagle_kill[4]:9:1,F_eagle_kill[5]:8:1,F_eagle_kill[6]:9:1,F_eagle_kill[7]:9:1,F_eagle_kill[8]:9:1,
     F_eagle_kill[9]:9:1,F_eagle_kill[10]:9:1,F_eagle_kill[11]:9:1,F_eagle_kill[12]:9:1);
   writeln(outagepr_out,-M_eagle_kill[0]:9:1,-M_eagle_kill[1]:9:1,-M_eagle_kill[2]:9:1,-M_eagle_kill[3]:9:1,
     -M_eagle_kill[4]:9:1,-M_eagle_kill[5]:9:1,-M_eagle_kill[6]:9:1,-M_eagle_kill[7]:9:1,-M_eagle_kill[8]:9:1,
     -M_eagle_kill[9]:9:1,-M_eagle_kill[10]:9:1,-M_eagle_kill[11]:9:1,-M_eagle_kill[12]:9:1);
   write(outagest_out,year:4,No_Hyrax_prev:11:1,F_next[0]:9:1,F_next[1]:9:1,F_next[2]:9:1,F_next[3]:9:1,F_next[4]:9:1,
     F_next[5]:8:1,F_next[6]:9:1,F_next[7]:9:1,F_next[8]:9:1,
     F_next[9]:9:1,F_next[10]:9:1,F_next[11]:9:1,F_next[12]:9:1);
   writeln(outagest_out,-M_next[0]:9:1,-M_next[1]:9:1,-M_next[2]:9:1,-M_next[3]:9:1,-M_next[4]:9:1,
     -M_next[5]:9:1,-M_next[6]:9:1,-M_next[7]:9:1,-M_next[8]:9:1,
     -M_next[9]:9:1,-M_next[10]:9:1,-M_next[11]:9:1,-M_next[12]:9:1,
     SR:7:4,fjuv:7:4,fimm:7:4,f2yr:7:4,fads:7:4,fold:7:4);
  until (year = end_date) or (terminate_model = TRUE);
close(outmain_out);                                                 { Close down the program and output files }
close(outagest_out);
close(outagepr_out);
writeln('DONE');
end.
```

University of Pretoria etd – Davies, R A G (1994)

# APPENDIX 11

## POSTAL ADDRESSES OF ALL PERSONS CITED 'PERS. COMM.' OR *'IN LITT.'* IN THIS THESIS

Mr. D.G. Allan, Avian Demography Unit, University of Cape Town, Rondebosch 7700, South Africa.

Mr. M. Anderson, Cape Nature Conservation, Private Bag X6102, Kimberley 8300, South Africa.

Mr. G.E.A. Banfield, Matobo Black Eeagle Survey, 49A, Lawley Road, Suburbs, Bulawayo, Zimbabwe.

Prof. R. Barry Jnr., Biology Dept., Frostberg State University, Frostburg, Maryland 21532-1099, U.S.A.

Mr. S.J. Bekker, Cape Nature Conservation, Priv. Bag X6546, George 6530, South Africa.

Mr. P. Benadie, Karoo National Park, P.O. Box 316, Beaufort West 6970, South Africa.

Dr. P. Benson, Dept. Zoology, Univ. of Witwatersrand, P.O. Wits 2001, South Africa.

Dr. A.F. Boshoff, Cape Nature Conservation, Private Bag 1126, Port Elizabeth 6000, South Africa.

Mr. A. Bowland, 32 Kilburn Ave., Durban, Natal, South Africa.

Dr. C.J. Brown, Directorate of Nature Conservation & Recreation Research, Priv. Bag 13306, Windhoek 9000, Namibia.

Mr. W.S. Clark, 4554 Shetland Green Road, Alexandria VA 22312, U.S.A.

Mr. D. Conroy, 'Mon Desir', Hutchinson, near Victoria West 7080, Cape Province, South Africa.

Mr. R.J.M. Crawford, Sea Fisheries Res. Inst., Roggebaii 8012, Cape Town, South Africa.

Dept. Agric., Middelburg, Private Bag X529, Middelburg 5900, South Africa.

Dr. H. Erasmus, Cape Nature Conservation, Private Bag X6102, Kimberley 8300, South Africa.

Mr. N. Esterhuizen, Cape Nature Conservation, Private Bag X6102, Kimberley 8300, South Africa.

Dr. N. Fairall, Jonkershoek Nature Conservation Station, Private Bag 5D14, Stellenbosch 7600, South Africa.

Mrs. V. Gargett, 12 Charles Veale Drive, West Beach SA 5024, Australia.

Dr. A.C. Kemp, Department of Birds, Transvaal Museum, P.O. Box 413, Pretoria 0001, South Africa.

Dr. R.G. Klein, The University of Chicago, Dept. Anthropology, 1126 East 59th St., Chicago, IL 60637, U.S.A.

Dr. M. Knight, National Parks Board Kimberley Office, P.O. Box 110040, Haddison Park 8306, South Africa.

Dr. J. Lindesay, Climatology Research Group, University of the Witwatersrand, Johannesburg 2001, South Africa.

Dr. R. Liversidge, 92 Central Road, Kimberley 8301, South Africa.

Mr. C. Mocke, Paardefontein, Beaufort West 6970, South Africa.

Mr. L.C. Moolman, Addo National Park, P.O. Box 52, Addo 6105, South Africa.

Mr. A.G. Morgan, P.O. Box 71, Steclestroom 5425, South Africa.

Mr. D. Nel, Kookfontein, Beaufort West 6970, South Africa.

Dr. P. Norton, Cape Nature Conservation, Private Bag 1126, Port Elizabeth 6000, South Africa.

Dr. P. Novellie, National Parks Board Kimberley Office, P.O. Box 110040, Haddison Park 8306, South Africa.

Mr. D.J. Olivier, Dept. Agric., Middelburg, Private Bag X529, Middelburg 5900, South Africa.

Mr. D. Pepler, Dept. Nature Conservation & Forestry, University of Stellenbosch, Stellenbosch 7600, South Africa.

Dr. R.M. Randall, National Parks Board, P.O. Box 774, George 6530, South Africa.

Mr. D. Shearing, Layton, Fraserberg, Cape Province, South Africa.

Prof. W.R. Siegfried, Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa.

Mr. C. Skinner, c/o 44 King Street, Irene 1675, South Africa.

Mr. J.H. Swiegers, Montana, Victoria West 7080, South Africa.

Dr. J.M. Thiollay, Ecole Normale Superieure, CNRS-UA258 Laboratoire d'Ecologie, 46, Rue d'Ulm, 75230 Paris Cedex 05, France.

Ms. F. van Heerden, Wilderness National Park, Private Bag X6528, George 6530, South Africa.

Mr. C. Webber, Geography Dept., Johannesburg College of Education, 27 St. Andrews Road, Parktown 2193, South Africa.

Mr. R. Wilmot, Paardekraal, P.O. Box 1109, Beaufort West, 6970, South Africa.