

**Factors influencing productivity in sympatric populations of
Mountain Reedbuck and Grey Rhebok in the Sterkfontein
Dam Nature Reserve, South Africa**

By

William Andrew Taylor

Submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

in the

Department of Tropical Diseases
Faculty of Veterinary Science
University of Pretoria
Pretoria

March 2004

**Factors influencing productivity in sympatric populations of
Mountain Reedbuck and Grey Rhebok in the Sterkfontein
Dam Nature Reserve, South Africa**

By William Andrew Taylor

Supervisor: Professor J.D. Skinner
Veterinary Wildlife Unit
Faculty of Veterinary Science
Onderstepoort

Co-supervisor: Professor R.C. Krecek
Department of Zoology and Entomology
Faculty of Natural and Agricultural Sciences
University of Pretoria

ABSTRACT

Productivity of grey rhebok and mountain reedbuck was studied at Sterkfontein Dam Nature Reserve (eastern Free State) between September 1999 and May 2002. Within a study area of 550 ha, all herds of grey rhebok and all territorial male mountain reedbuck were identified, and general population dynamics were monitored. Lambs of both species were born seasonally between September and February, while most deaths occurred between June and November. Population levels appeared to be controlled in both species mainly by the eviction of young males, but the effects of extreme weather conditions were significant, being demonstrated by the deaths of 27 % and 51 % of the grey rhebok and mountain reedbuck populations respectively during heavy snow in September 2001. Disease and predation played no role in population control. Grey rhebok formed stable harem herds with home ranges varying between 23 ha and 104 ha (95 % MCP), with an average of 57.9 ha. Home ranges in

areas with extensive steep slopes tended to be smaller than those in flatter areas. The ecological density was 1/15.7 ha. Territorial male mountain reedbuck were often solitary, and only accompanied by females when these moved into their territories. Home ranges of males varied between 7 ha and 21 ha (95 % MCP), with an average of 14.8 ha, and all had areas of steep slopes within. Females showed strong preference for steep slopes and used much greater areas than males. The ecological density was 1/8.7 ha.

Grey rhebok rested less than mountain reedbuck, but did not feed for longer. Grey rhebok were active intermittently all day and night, but tended to be more active in the early morning and late afternoon than in the middle of the day. During the day, mountain reedbuck were most active in the late afternoon, rested for longer periods in the middle of the day, but were also very active at night. Body condition was investigated seasonally in mountain reedbuck at Sterkfontein and also Tussen die Riviere Nature Reserve. Kidney fat indices and leg fat percentages were lowest at the end of winter before the rains started and when the nutritive value of the veld was at its lowest. Endoparasites were investigated in both antelope species, but primarily in mountain reedbuck. Seventeen species of helminths, including fifteen nematodes, one trematode, and one cestode were recovered from mountain reedbuck at Sterkfontein and TdR. The most prevalent and abundant species were *Cooperia yoshidai*, *Longistrongylus schrenki* and *Haemonchus contortus*. Five nematode species were recovered from four grey rhebok at Sterkfontein.

Key words: Grey rhebok, *Pelea capreolus*, mountain reedbuck, *Redunca fulvorufula*, productivity, population dynamics, home ranges, behaviour, body condition, nematodes.

ACKNOWLEDGEMENTS

I would first like to thank my supervisor Professor John Skinner for advising and encouraging me through the duration of this study. I have been with Prof Skinner for nearly eight years, first as a M.Sc. student, and now as a doctoral student and have been very fortunate to be able to make use of his vast zoological knowledge and experience.

Professor Tammi Krecek has acted as my co-supervisor for the project, and I am very grateful to her for securing me an NRF bursary, for making sure I was up to date with various reports, and for her all-round general support throughout.

A very special thank you to the Roods family, Mark, Tracey, Michéle and Jonathan, for allowing me to stay with them and for making my life a lot more enjoyable than it would have been had I stayed on my own. Their generosity went far beyond the call of duty, as they fed me very satisfying meals every day, let me watch TV with them, and always made me feel part of the family. In addition to this, Mark, as the Reserve Manager of Sterkfontein, was always very supportive of the project and went out of his way to assist me whenever he could.

I received important academic and practical help from the following people: Professor Joop Boomker gave advice during the planning stages of the project and identified some of the more difficult nematode species, including the new species; Ryno Watermeyer identified many of the nematode species for me and patiently helped me learn to ID the worms myself; Dawn Durand showed me how to do larval nematode culture; and Professor Mark Williams enthusiastically helped me prepare to conduct necropsies and performed histopathology analysis on all samples I collected.

Professor Woody Meltzer was Head of the Veterinary Wildlife Unit when I started, and provided project advice and logistical assistance. Professor Henk Bertschinger took over the reigns of the Unit at a later stage and also provided assistance. Ellen Nel provided secretarial assistance and kept tabs on my budget.

Cedric Barbé ably assisted me in collecting observational data and biological material from culled animals during 1999, and Dominic Moss assisted me with darting mountain reedbuck and also with culling and dissecting animals early in the study. Colin Oliver and Melvyn Quan helped me collar young grey rhebok males that proved very useful when it came time for young males to be evicted from their natal herds, and Colin also helped with collection of biological material. Thanks also to Illius (the late gardener) for meticulously helping me dissect mountain reedbuck legs.

Free State DEAT (Nature Conservation) kindly allowed me to conduct the research on their Provincial Nature Reserves. Savvas Vrahimis supported the project from the outset, and was very helpful in getting the relevant permission to conduct the research. Francois Nieuwoudt acted as a shottist for a large number of the culled reedbuck, and performed the task very proficiently. Nacelle Collins assisted in a number of ways, including providing access to useful reserve data and vital email. Francois van den Berg provided culled and hunted mountain reedbuck from Tussen die Riviere, from which I got considerable biological material. The Free State game capture team captured and collared mountain reedbuck and grey rhebok during translocation experiments.

Hector Dott, Marie Smith, and Adam Butler provided me with useful statistical advice during the write up of my thesis. Malcolm Rutherford and Derek Pettitt at River Bend kindly allowed me to complete the write up of my thesis while taking up employment at River Bend Conservancy.

The National Research Foundation generously provided me with Ph.D. bursaries for three years under their research theme at the Faculty of Veterinary Science aimed at the improvement in quality of life, while the research committee of the faculty of Veterinary Science, Onderstepoort provided important funding for the project. I was also very grateful to the Blundell Memorial scholarship and the Maberly Memorial scholarship, both of which provided me bursaries for three years.

Finally, I would like to thank my parents for their constant love, support and encouragement throughout my studies, and for assisting me financially on many occasions. I dedicate this work to my Father, who died on 4 August 2003.

Table of Contents

CHAPTER 1. INTRODUCTION	1
AIMS	4
CHAPTER 2. STUDY SITES	7
Sterkfontein Dam Nature Reserve	7
Tussen die Riviere Nature Reserve	11
CHAPTER 3. POPULATION DYNAMICS	14
Introduction	14
Methods	16
<i>Study site and animals</i>	16
<i>Changes in population size</i>	18
<i>Monitoring deaths and disease</i>	19
Results	21
<i>Births</i>	21
<i>Deaths</i>	24
<i>Immigration and emigration</i>	29
<i>Overall population dynamics</i>	31
<i>Helicopter counts</i>	33
Discussion	34
<i>Births</i>	34
<i>Deaths</i>	36
<i>Dispersal</i>	40
<i>Translocations</i>	43
<i>Aerial counts</i>	44
<i>Overall trends</i>	44
CHAPTER 4. HOME RANGES AND HABITAT	46
Introduction	46
Methods	48
<i>Study site and animals</i>	48
<i>Geographic positions</i>	48
<i>Home range estimation</i>	49
<i>Vegetation surveys</i>	51
<i>Investigating causes of variation in home range sizes</i>	51
<i>Statistical methods</i>	53
Results	54
<i>Accumulative home range area graphs</i>	54
<i>Home ranges areas</i>	54
<i>Ecological densities</i>	63
<i>Vegetation surveys</i>	63
<i>Causes of variation in home range size</i>	64
Discussion	66
<i>Home range areas</i>	66
<i>Vegetation surveys</i>	68
<i>Causes of variation in home range size</i>	69
<i>Interspecific comparison of home range size</i>	70

CHAPTER 5. ACTIVITY PATTERNS, FORAGING BEHAVIOUR AND SOCIAL BEHAVIOUR.....	72
Introduction.....	72
Methods.....	74
<i>Study site and animals</i>	74
<i>Behaviour</i>	74
<i>Activity budgets and activity patterns</i>	77
<i>Territorial marking</i>	77
<i>Statistical methods</i>	78
Results.....	78
<i>Diurnal activity budgets</i>	78
<i>Diurnal activity patterns</i>	81
<i>Patterns of activity and inactivity</i>	87
<i>Nocturnal activity patterns</i>	87
<i>Ruminating and drinking</i>	88
<i>Male reproductive behaviour</i>	89
<i>Territorial marking and territory patrols</i>	91
<i>Juvenile submission</i>	94
<i>Eviction of juveniles</i>	96
Discussion.....	98
<i>Activity budgets</i>	98
<i>Diurnal activity patterns</i>	99
<i>Nocturnal activity patterns</i>	102
<i>Ruminating and drinking</i>	102
<i>Male reproductive behaviour</i>	103
<i>Territorial marking and territory patrols</i>	105
<i>Juvenile submission</i>	107
<i>Eviction of juveniles</i>	108
CHAPTER 6. BODY CONDITION.....	109
Introduction.....	109
Methods.....	114
<i>Study site and animals</i>	114
<i>Body condition indices</i>	115
<i>Statistical methods</i>	116
Results.....	117
<i>Sterkfontein Dam Nature Reserve</i>	117
<i>Carcass weights and dressing percentages</i>	117
<i>Regression analysis of kidney weight and body weight</i>	118
<i>Regression of LFP on KFI</i>	120
<i>Variation in body condition from KFI and LFP</i>	121
<i>Tussen die Riviere Nature Reserve</i>	125
<i>KFI and endoparasitic nematodes</i>	126
Discussion	127
<i>Carcass weights</i>	127
<i>Dressing percentages</i>	128
<i>Regression analysis of kidney weight and body weight</i>	130
<i>Variation in body condition from KFI and LFP</i>	130
<i>KFI and endoparasitic nematodes</i>	136

CHAPTER 7. PARASITES.....	137
Introduction.....	137
Methods.....	139
<i>Study sites and animals</i>	139
<i>Recovery of alimentary helminths</i>	140
<i>Helminths of the heart, lungs and liver</i>	141
<i>Worm identification and quantification</i>	141
<i>Faecal egg counts</i>	142
<i>Coproculture</i>	143
<i>Statistical methods</i>	143
Results.....	144
<i>Helminth species prevalence and abundance</i>	144
<i>Frequency distributions of nematodes at Sterkfontein</i>	146
<i>Abomasum nematodes at Sterkfontein</i>	147
<i>Small intestine nematodes at Sterkfontein</i>	151
<i>Large intestine nematodes at Sterkfontein</i>	152
<i>Age differences</i>	153
<i>Host body condition (kidney fat index)</i>	154
<i>Nematodes and pregnancy</i>	155
<i>Nematodes of Tussen die Riviere</i>	155
<i>Nematodes of grey rhebok at Sterkfontein</i>	156
<i>Faecal egg counts and coproculture in mountain reedbuck</i>	157
<i>Faecal egg counts and coproculture in grey rhebok</i>	158
Discussion.....	159
<i>Species prevalence and abundance</i>	159
<i>Frequency distributions of nematodes</i>	159
<i>Possible causes of aggregation</i>	161
<i>Cross-transmission with domestic livestock</i>	165
<i>Nematodes of Tussen die Riviere</i>	167
<i>Nematodes of grey rhebok at Sterkfontein</i>	167
CONCLUSIONS.....	169
SUMMARY.....	174
REFERENCES.....	180
APPENDIX I.....	191
Accumulative home range areas for grey rhebok herds.....	191
APPENDIX I (CONTINUED).....	192
Accumulative home range areas for mountain reedbuck males.....	192
APPENDIX I (CONTINUED).....	193
Accumulative home range areas for mountain reedbuck males.....	193
APPENDIX II.....	194
Summary comparisons for grey rhebok and mountain reedbuck at Sterkfontein Dam Nature Reserve.....	194
APPENDIX II (CONTINUED).....	195
Summary comparisons for grey rhebok and mountain reedbuck at Sterkfontein Dam Nature Reserve.....	195

List of Figures

Figure 1. The geographic distribution of grey rhebok and southern mountain reedbuck within South Africa. 1

Figure 2. Sterkfontein Dam Nature Reserve. 8

Figure 3. Climatic variables of Sterkfontein Dam Nature Reserve: (a) Maximum and minimum temperatures; (b) Average rainfall over 25 years between 1977 and 2002; (c) Rainfall in main study site during the study period..... 9

Figure 4. Tussen die Riviere Provincial Nature Reserve. 12

Figure 5. Climatic variables of Tussen die Riviere: (a) Maximum and minimum temperatures, (b) average rainfall for 23 years. Recorded at Goedemoed..... 13

Figure 6. Grey rhebok births for three lambing seasons at Sterkfontein between September 1999 and July 2002. Data were from direct observations of live animals. 22

Figure 7. Mountain reedbuck birth months at Sterkfontein, obtained by extrapolation of foetus masses using the Hugget & Widdas (1951) formula, adapted for mountain reedbuck by Norton (1989). 24

Figure 8. The population dynamics of all grey rhebok within the main study area at Sterkfontein between September 1999 and July 2002. Up arrows indicate increases in population; down arrows indicate decreases. Letters indicate reasons for change: A = birth, B = natural death, C = accidental death, D = snow death, E = eviction of young male, F = eviction of young female, G = disappearance of animal for unknown reason, H = immigration. 32

Figure 9. Population dynamics of mountain reedbuck within the main study area at Sterkfontein between February 2000 and April 2002. Error bars represent estimated counting errors. 33

Figure 10. Home ranges of six harem herds of grey rhebok in the main study area of Sterkfontein between February 2000 and April 2002. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 75 % and 50 % AK results. 57

Figure 11. Grey rhebok home ranges and steep slopes (>10°) in the main study area at Sterkfontein. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results. 59

Figure 12. Home ranges of 10 territorial male mountain reedbeek in the main study area between February 2000 and April 2002, superimposed over steep slope (>10°). External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results.....	60
Figure 13. The space use of three mountain reedbeek females within the main study area.....	61
Figure 14. Home range overlap between grey rhebok herds and territorial male mountain reedbeek in the main study area between February 2000 and April 2002.....	62
Figure 15. Activity budgets of grey rhebok at Sterkfontein: (a) males; (b) females. .	79
Figure 16. Activity budgets of mountain reedbeek at Sterkfontein: (a) males; (b) females.....	80
Figure 17. The diurnal activity patterns of male grey rhebok: (a) November to February; (b) May to August.	81
Figure 18. The diurnal activity patterns of female grey rhebok: (a) November to February; (b) May to August.	82
Figure 19. The diurnal activity patterns of male mountain reedbeek: (a) November to February; (b) May to August.	83
Figure 20. The diurnal activity patterns of female mountain reedbeek: (a) November to February; (b) May to August.	84
Figure 21. The nocturnal activity patterns of grey rhebok and mountain reedbeek at Sterkfontein.....	88
Figure 22. Number of drinking observations made on grey rhebok between January 2000 and December 2001.	89
Figure 23. Average monthly frequency of territorial patrols by harem male grey rhebok at Sterkfontein. N = 5 males. Error bars represent standard error.	94
Figure 24. Variation in the frequency of submission in male grey rhebok lambs with increasing age. Error bars represent standard error.	95
Figure 25. Seasonal variation in dressing percentages of male (n = 16) and female (n = 17) mountain reedbeek at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.....	117

Figure 26. Log-log linear regression of mountain reedbuck body weight against kidney weight at Sterkfontein. (a) All animals (b) animals less than 20 kg excluded.	119
Figure 27. Seasonal variation in KW of mountain reedbuck at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.....	120
Figure 28. Linear regression comparing KFI with LFP in mountain reedbuck at Sterkfontein (n = 39).....	121
Figure 29. Seasonal variation in (a) KFI and (b) LFP for male and female mountain reedbuck at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error..	122
Figure 30. Linear regression comparing mountain reedbuck body weight with KFI for (a) males at Sterkfontein and TdR (b) females at Sterkfontein and TdR. Animals under 20 kg were excluded..	124
Figure 31. Seasonal variation in KFI for male and female mountain reedbuck at TdR. Error bars represent standard error.	125
Figure 32. Scatter plots of KFI against (a) number of nematodes in the abomasum, (b) number of nematodes in the SI, (c) number of nematodes in the LI.	127
Figure 33. Observed frequency distributions of (a) <i>H. contortus</i> , (b) <i>L. schrenki</i> , (c) <i>Cooperia</i> spp. and (d) <i>Skrjabinema</i> sp. found in 41 mountain reedbuck culled at Sterkfontein between March 2000 and February 2002. <i>k</i> = the corrected moment estimate for aggregation.....	147
Figure 34. Seasonal variation in (a) <i>Haemonchus contortus</i> and (b) <i>Longistrongylus schrenki</i> in the abomasums of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender and per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.	149
Figure 35. Seasonal variation in <i>Cooperia</i> spp. in the small intestines of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.....	151

- Figure 36.** Seasonal variation in *Skrjabinema* sp. in the large intestines of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error. 153
- Figure 37.** Scatter plots of kidney fat index against (a) number of nematodes in the abomasum, (b) number of nematodes in the small intestine, (c) number of nematodes in the small intestine. 154
- Figure 38.** Seasonal variation in (a) *H. contortus*, (b) *T. falculatus*, (c) *N. spathiger*, and (d) *C. rotundispiculum* in 14 male and 11 female mountain reedbuck at TdR in one summer (December 1999) and two winter (June 2000, 2001) periods. Error bars represent standard error. 156
- Figure 39.** Monthly variation in nematode larval counts from coproculture of faeces from five grey rhebok at Sterkfontein between September 2001 and April 2002. Numbers of larvae were adjusted for 100 g faeces. 158

List of Tables

Table 1. Grey rhebok birth records, lamb sex ratios and adult female numbers separated into herds between 1999 and 2002.22

Table 2. Pregnancy records of mountain reedback from culled females and females that died of hypothermia (*) at Sterkfontein in 2000 and 2001.25

Table 3. Mortality records of grey rhebok in the main study area at Sterkfontein between October 1999 and April 2002.26

Table 4. Mortality records of mountain reedback in the main study area at Sterkfontein between February 2000 and April 2002. * = animals that had been introduced from Caledon Nature Reserve.....27

Table 5. Mortality rates of ungulates in the main study area during the snowfall of September 2001. Numbers do not include lambs less than three months age.28

Table 6. Comparison of counts of grey rhebok and mountain reedback using two different techniques: helicopter counts and long term ground counts.33

Table 7. Home ranges of six grey rhebok harem herds between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel.....55

Table 8. Seasonal variation in home range areas of four grey rhebok herds.55

Table 9. Home ranges of 10 territorial male mountain reedback between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel, * = asymptote not achieved.....56

Table 10. Grass and forb densities on steep slopes and flat ground in five survey areas, given as the average distances to the nearest grasses and forbs. Standard deviations are in parentheses.63

Table 11. Two-way ANOVA comparing grass and forb densities within steep and flat areas..... 64

Table 12. Parameters selected to test for predictor variables for home range areas for grey rhebok herds.....65

Table 13. Parameters selected to test for predictor variables for home range areas for territorial male mountain reedback.....65

Table 14. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (of both genders) and between periods of the day in the time spent resting. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck. Data were arcsine transformed.	86
Table 15. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (including genders) and between periods of the day in the time spent feeding. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck. Data were arcsine transformed.	86
Table 16. Average hourly frequency of territorial marking by three harem male grey rhebok over three time periods.	92
Table 17. Two way ANOVA comparing the frequency of territorial marking by three harem male grey rhebok over three time periods. Data were log ₁₀ transformed.	93
Table 18. Two-way ANOVA comparing the differences in frequency of submissive behaviour between three groups and three age categories (2 – 5 months, 5 – 8 months, 8 – 11 months) of male grey rhebok lambs.	96
Table 19. Eviction dates for 13 juvenile male grey rhebok.	96
Table 20. Two-way ANOVA comparing dressing percentages of 33 mountain reedbuck between gender (16M: 17F) and between seasons at Sterkfontein.	118
Table 21. Two-way ANOVA comparing KW of 38 mountain reedbuck between gender (M18: F20) and seasons at Sterkfontein.	119
Table 22. Two-way ANOVA comparing KFI of 38 mountain reedbuck between gender (18M: 20F) and between seasons at Sterkfontein. Data was Log ₁₀ transformed.	123
Table 23. Two-way ANOVA comparing LFP of 39 mountain reedbuck between gender (20M: 19F) and between seasons at Sterkfontein. Data were arcsine transformed.	123
Table 24. Two-way ANOVA comparing KFI of mountain reedbuck between gender and between seasons at TdR. Data were Log ₁₀ transformed.	126

Table 25. Prevalence and abundance of helminths recovered from 41 mountain reedbuck culled at Sterkfontein between March 2000 and February 2002. (Prev. = prevalence, Std. Dev. = standard deviation, T = trematode, N = nematode, C = cestode, L ₄ = fourth larval stage, Rum = rumen, Abo = abomasum, SI = small intestine, LI = large intestine, * = new species).....	145
Table 26. Prevalence and abundance of helminths recovered from mountain reedbuck at TdR between December 1999 and June 2001. (Prev = prevalence, Std. Dev. = standard deviation, T = trematode, N = nematode, C = cestode, Rum = rumen, Abo = abomasum, SI = small intestine, LI = large intestine, Vis = visceral cavity).	146
Table 27. Two-way ANOVA comparing the differences between genders and between months in the numbers of <i>H. contortus</i> in 41 mountain reedbuck at Sterkfontein. Data were Log ₁₀ transformed.	150
Table 28. Two-way ANOVA comparing the differences between genders and between months in the numbers of <i>L. schrenki</i> in 41 mountain reedbuck at Sterkfontein. Data were Log ₁₀ transformed.	150
Table 29. Two-way ANOVA comparing differences between genders and between months in the numbers of <i>Cooperia</i> spp. in 41 mountain reedbuck at Sterkfontein. Data were Log ₁₀ transformed.	152
Table 30. Prevalence and abundance of nematodes recovered from four grey rhebok at Sterkfontein in 2001 (Prev = prevalence, Std. Dev. = standard deviation, Abo = abomasum, SI = small intestine).....	157
Table 31. Spearman Rank Correlation Coefficient comparing faecal egg counts, number of larvae in faeces from coproculture, and the actual number of nematodes found in the GIT of 18 mountain reedbuck at Sterkfontein.....	157