

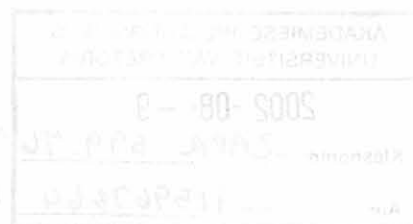
**Feeding ecology and social organisation of honey badgers  
(*Mellivora capensis*) in the southern Kalahari.**

by

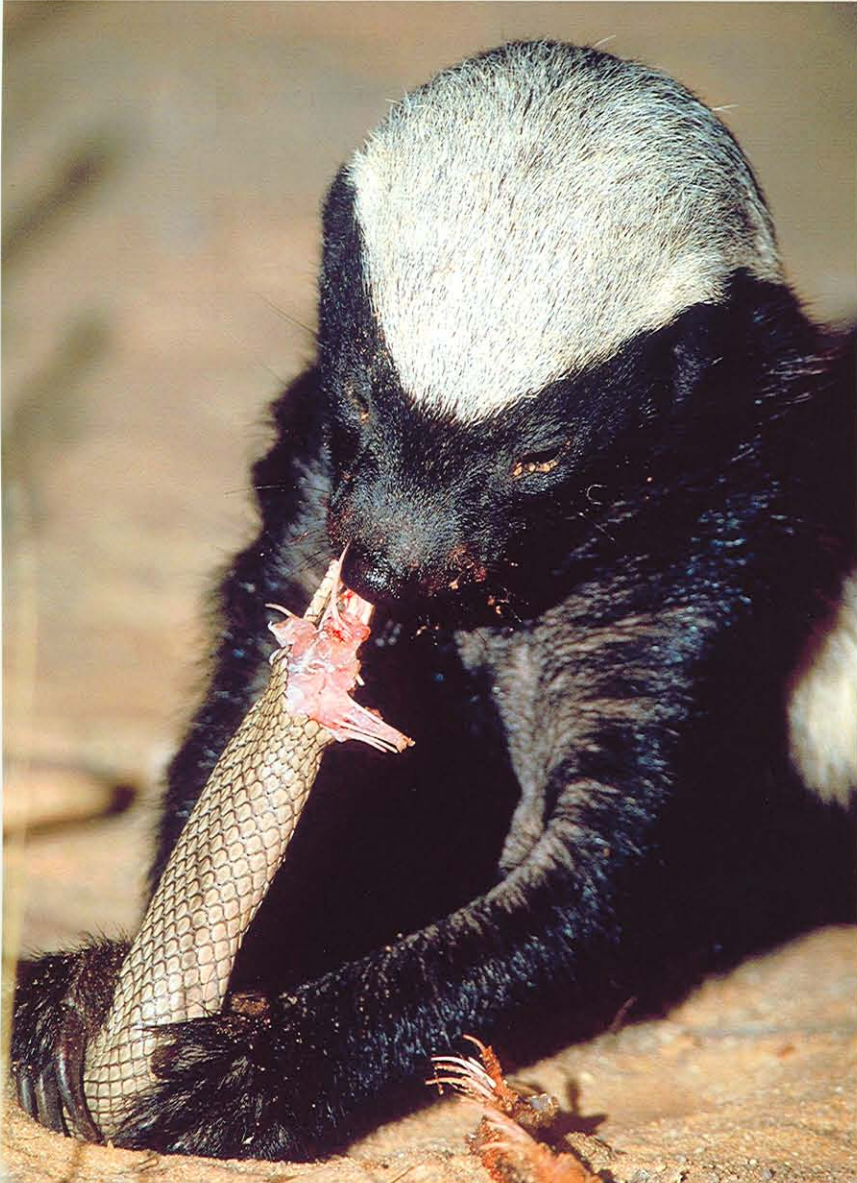
**Colleen Margaret Begg**

Submitted in partial fulfillment of the requirements for the degree of  
Doctor of Philosophy (Zoology)  
in the Faculty of Natural and Agricultural Sciences  
University of Pretoria  
Pretoria

November 2001



**For Keith, who started it all.**



Female honey badger eating a mole snake

**Feeding ecology and social organisation of honey badgers  
(*Mellivora capensis*) in the southern Kalahari**

**Colleen Margaret Begg**

Supervisors: Prof. J.T. du Toit

Director: Mammal Research Institute

Department of Zoology and Entomology

University of Pretoria

Prof. M.G.L. Mills

Specialist Scientist: Kruger National Park

Carnivore Conservation Group, Endangered Wildlife Trust

Submitted for the degree of Doctor of Philosophy (Zoology) in the Faculty of Natural & Agricultural Sciences.

**Summary**

The lack of fundamental biological information on the honey badger *Mellivora capensis* and its vulnerable conservation status were the motivating factors behind this study. A study population of 25 individuals (12 females; 12 males) was radio-marked in the Kgalagadi Transfrontier Park (KTP), South Africa. Through a combination of radio telemetry and visual observations (5 244 h) of nine habituated individuals (five females; four males), the feeding ecology, scent marking and social behaviour of the honey badger were investigated.

The honey badger is a solitary, generalist carnivore with strong seasonal differences in diet. In support of optimal diet theory, the cold dry season diet is characterized by low species richness, low foraging yield, high dietary diversity and increased foraging time while the reverse is true in the hot wet and hot-dry seasons. The honey badger appears to shift between alternative prey species depending on their availability on a seasonal and daily level. The

daily activity patterns of both sexes show a strong seasonal shift from predominantly nocturnal activity in the hot-wet and hot-dry season to more diurnal activity in the cold-dry season and this appears to be primarily affected by temperature.

Despite marked sexual size dimorphism (males a third larger than females), no intersexual differences in diet or foraging behaviour were observed, but there were sexual and in males age-related differences in movement patterns, scent marking and social behaviour. The honey badger appears to have a polygynous or promiscuous mating system, but did not fit the general mustelid pattern of intrasexual territoriality. Instead, adult males had extensive overlapping home ranges (548 km<sup>2</sup>) that encompassed the smaller, regularly spaced home ranges of the females (138 km<sup>2</sup>) and young males (178 km<sup>2</sup>). Receptive females are an unpredictable and scarce resource in space (large home ranges) and time (no breeding season) with a long time to renewal (inter-birth interval > 1 year). As a result adult males adopt a roaming rather than a staying tactic with competition for access to the mating burrow mediated by a dominance hierarchy loosely based on age, mass and testes size. The hierarchy appears to be maintained through regular aggressive and agonistic interactions and scent marking. Data suggest that latrine scent marking in adult males is related to advertising social status and maintaining the dominance hierarchy through “scent matching”. In females and young males latrine visits are rare, but token urination is common and its association with foraging behaviour suggests that it mediates spatio-temporal separation and/or resource utilization.

Interspecific interactions between the honey badger and other mammalian and avian predators were common and included intraguild predation and interspecific feeding associations between the honey badger and seven other species (two mammals; five birds). The most common foraging associations were observed between the honey badger and the pale

chanting-goshawk *Melierax canorus* and black-backed jackal *Canis mesomelas*. These associations appear to be commensalism, with associating species benefiting from increased hunting opportunities and intake rate but no significant costs or benefits to the honey badger.

you.

I would like to express my appreciation to South African National Parks and the warden of the Kalahari Gemsbok Park, Dries Engelbrecht for permission to work in this extraordinary wilderness area. Thank you to all the National Parks staff who helped in a myriad of ways during the course of the fieldwork, in particular Dr Mike Knight, Liz Quin-Costley, Ingrid Novellie, Max H. Engelbrecht, Giel and Renée de Kock and Yon Piel Krüper. I am particularly indebted to Titaine and Leticia Visser, who allowed us to set up a base camp in Mata Mata, for their hospitality, and constant support of the project. Thank you to Giel, Giel de Kock and Max H. Engelbrecht for all the time and effort they put into helping us find wayward badgers from the air.

The project was supported and administered by the Carnegie Corporation, through the Endangered Wildlife Trust. In particular, I thank the director Dr John Ledger for supporting the project from its inception, Dr Gus Mills for bringing the badger project under the UK umbrella and Pat Fischer for dealing with all our urgent requests from the Kalahari and keeping us informed of our financial situation.

I am most grateful to all our sponsors who kept us in the field: Southern Life Associated Ltd (Mr Q. Pretorius), First National Bank (Mr V. Bartlett), the Davies Foundation (Mr B. Yeoward), David & Carol Hughes, John Ruggieri, The Johannesburg Zoo (Dr Pat Lind) and the Friends of the Johannesburg Zoo Trust, Klatzo & Waldron (Mr R. Waldron), The Ripro Hotel, Potchefstroom (Kobus & Lorraine Peuris), Brooke Patrick Publications (John S

## Acknowledgements

My thanks go to all those that have helped, financially supported and encouraged me over the last four years of fieldwork and two years of writing up, it could not have been done without you.

I would like to express my appreciation to South African National Parks and the warden of the Kalahari Gemsbok Park, Dries Engelbrecht for permission to work in this extraordinary wilderness area. Thank you to all the National Parks staff who helped in a myriad of ways during the course of the fieldwork, in particular Dr Mike Knight, Dr Guy Castley, Dr P Novellie, Mrs H. Engelbrecht, Giel and Rentia de Kock and Vet Piet Kruiper. I am particularly indebted to Tiennie and Lettie Visser, who allowed us to set up a base camp in Mata Mata, for their hospitality, and unstinting support of the project. Thank you to the pilots Giel de Kock and Martin Engelbrecht for all the time and effort they put into helping me find wayward badgers from the air.

The project was supported and administered by the Carnivore Conservation Group of the Endangered Wildlife Trust. In particular, I thank the director Dr John Ledger for supporting the project from its inception, Dr. Gus Mills for bringing the badger project in under the CCG umbrella and Pat Fletcher for dealing with all our urgent requests from the Kalahari and keeping us informed of our financial situation.

I am most grateful to all our sponsors who kept us in the field: Southern Life Associated Ltd (Mr Q. Pretorius); First National Bank (Mr V. Bartlett); the Davies Foundation (Mr B. Yeowart); David & Carol Hughes; John Ruggieri; The Johannesburg Zoo (Dr Pat Condy) and the Friends of the Johannesburg Zoo Trust; Klatzo & Waldron (Mr. R. Waldron); The Elgro Hotel, Potchefstroom (Kobus & Lorraine Fourie), Brooke Patrick Publications (John &

Maureen Patrick); Neil Muller Construction; Environmental Advisory Services (Dr G. Begg); Air BP Africa (Mr H. Parboo; Mr A. Mocke); Engen Petroleum Ltd; Beith Digital CC (Mr D. da Silva); Foto Distributors – Nikon (Mr B. Schawrtz & Mr J. Pretorius). Particular thanks to the University of Pretoria, the National Research Foundation and the Carnivore Conservation Group for funding the writing up period.

Thanks are also due to all those that gave donations and equipment for the project particularly Osmond, Lange & Mosienyane (Mr D. van Onselen); Mike Devlin; L.R. Foam (Harvey family); Bridge-House School; Postnet Rondebsoch (Jonathan & Val Wild); Clem Haagner; Steve & Wendy Kalb; Flip & Jane Sheridan; Oom Piet Heymans and Tony & Sharon Heald.

The project was supervised by Prof Johan Du Toit and Prof Gus Mills, and I am very grateful for all their encouragement, advice and red ink. Particular thanks to Gus who believed in and supervised the project from its inception, and spent so much time in the field with us helping us to interpret strange badger behaviour, despite the fact that he was seldom fed and was kept up all night. Special thanks to Johan who took me on at such a late stage, expertly guided me through another thesis and provided funding during the writing up.

I thank the wildlife vets; Dr Douw Grobler; Dr Pete Morkel; Dr Mike Kock and Dr Erick Verrenne who implanted the radio transmitters into the honey badgers for us, often under stressful circumstances, and Dr Emily Lane for her histopathological examination of the back scar. I am grateful to Dr Gerard Malan for commenting on some of the chapters, Dr G. Alexander, Dr B. Branch, Dr L. Prendini; Prof. Yom Tov, Prof J. Nel; Dr F. Cuzin for providing comments and information, Prof J. Juritz for statistical advice, Michael Hoffman for contacts in the rest of Africa, and Maartin Strauss for help with Ranges V software.

As always I thank my parents, for their unconditional support and encouragement and for providing a home base in Johannesburg during our regular visits; and to George and Lea Begg for understanding what it was all about, and for their unstinting support. Thank you to David and Carol Hughes for their valued friendship and for being the ones that shared all the agonies and triumphs in the Kalahari, for believing in us, for feeding us, for loaning us our first two vehicles and for sponsoring our telemetry and communications equipment.

I am indebted to the late Klaas Kruiper, Khomani San tracker, for his enthusiasm and untiring efforts to find honey badgers and interpret their spoor. He was instrumental in the initial capture of honey badgers and taught us a great deal about the Kalahari. Thank you also to the late Rickie Kruiper who interpreted spoor during the pilot study

Most importantly, I thank Keith, who started it all, believed I could do it, shared in every minute of the Kalahari honey badger project and kept me going during the writing up. These have been special times.

## Contents

Summary.....	iii
Acknowledgements.....	vi
Contents .....	ix
List of Tables.....	xiv
List of Figures.....	xix
List of Plates.....	xxvi
<b>CHAPTER 1: General introduction .....</b>	<b>1</b>
1.1 The honey badger, or ratel, <i>Mellivora capensis</i> (Schreber 1776): an overview.....	1
1.1.1 Phylogenetic relations .....	1
1.1.2. Geographical range and conservation status .....	3
1.1.3 Fact & Fiction .....	4
1.2 This study .....	9
1.2.1. Rationale .....	9
1.2.3. Objective .....	10
1.2.4 Key questions .....	10
1.2.5. Overview of the thesis .....	11
1.3. References .....	13
<b>CHAPTER 2: Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger <i>Mellivora capensis</i>.....</b>	<b>21</b>
2.1 Abstract .....	21
2.2 Introduction .....	22
2.3 Study area and methods .....	24
2.3.1 Study area .....	24
2.3.2 Climate .....	25
2.3.3 Data collection .....	27
2.3.4 Analysis .....	28
2.4 Results.....	31

2.4.1 Overall diet .....	31
2.4.2 Seasonal variation in diet .....	37
2.4.3 Annual changes .....	41
2.4.4 Sexual differences in body size, diet and foraging behaviour .....	44
2.4.5 Foraging behaviour .....	50
2.5 Discussion.....	57
2.6 References.....	63
<b>CHAPTER 3: Sexual and seasonal variation in the time budget and activity patterns of the honey badger <i>Mellivora capensis</i> in an arid environment.....</b>	<b>69</b>
3.1 Abstract .....	69
3.2 Introduction .....	70
3.3 Methods .....	72
3.3.1 Study area .....	72
3.3.2 Climate .....	72
3.3.3 Study population .....	73
3.3.4 Definition of terms .....	75
3.3.5 Data analysis .....	77
3.4 Results .....	78
3.4.1. Time budgets .....	78
3.4.2. Activity patterns .....	85
3.5. Discussion.....	98
3.5.1 Time budgets .....	98
3.5.2 Activity schedules .....	99
3.6. References .....	103
<b>CHAPTER 4: Interspecific interactions between the honey badger <i>Mellivora capensis</i> and other predators in the southern Kalahari: intraguild predation and facilitation.....</b>	<b>107</b>
4.1 Abstract .....	107
4.2 Introduction .....	108
4.3 Study area and methods.....	110
4.3.1 Study area .....	110
4.3.2 Data collection .....	111
4.3.3 Data analysis .....	112

4.4 Results .....	114
4.4.1 Overview .....	114
4.4.2 Overall foraging associations .....	118
4.4.3 Honey badgers and pale chanting-goshawks .....	120
4.4.4 Honey badger and black-backed jackal .....	126
4.4.5 Other associating species .....	129
4.4.6 Intraguild predation and aggressive interactions .....	130
4.5 Discussion .....	134
4.5.1. Foraging associations .....	134
4.5.2 Aggressive interactions .....	138
4.6 References .....	141
<b>CHAPTER 5: Spatial organisation of the honey badger <i>Mellivora capensis</i> in the southern Kalahari: factors affecting home range size and movement patterns.....</b>	<b>148</b>
5.1 Abstract .....	148
5.2 Introduction .....	149
5.3 Study area and methods .....	151
5.3.1 Study Area .....	151
5.3.2 Data collection .....	152
5.3.2 Data analysis .....	154
5.4 Results .....	155
5.4.1 Home range .....	155
5.4.2 Movement Patterns .....	168
5.5 Discussion .....	174
5.5.1 Female home range and movement patterns .....	174
5.5.2 Male home range and movement patterns .....	179
5.6 References .....	181
<b>CHAPTER 6: Scent marking behaviour of the honey badger <i>Mellivora capensis</i> (Mustelidae) in the southern Kalahari.....</b>	<b>187</b>
6.1. Abstract .....	187
6.2 Introduction .....	188
6.3 Study area and methods .....	190
6.3.1. Data collection .....	190

6.3.2. Data analysis .....	192
6.3.3. Hypotheses related to scent marking in non territorial carnivores .....	192
6.4. Results .....	193
6.4.1. Types of scent marking .....	193
6.4.2. Latrines .....	199
6.4.3. Token urination .....	211
6.4.4. Squat marking .....	214
6.5 Discussion .....	218
6.5.1. Latrines .....	219
6.5.2. Token urination .....	224
6.5.3. Squat marking .....	226
6.6 References .....	227
<b>CHAPTER 7: Breeding system and social interactions of the honey badger <i>Mellivora capensis</i> in the southern Kalahari.....</b>	<b>233</b>
7.1 Abstract .....	233
7.2 Introduction .....	234
7.3 Study area & Methods .....	236
7.3.1 Study Area .....	236
7.3.2 Data collection .....	237
7.4 Results .....	239
7.4.1 Life history characteristics .....	239
7.4.2 Wounds and scars .....	244
7.4.3 Male-male interactions .....	246
7.4.4 Age and size of interacting males .....	252
7.4.5 Intersexual interactions .....	259
7.5 Discussion .....	260
7.5.1 Reproduction and parental care .....	260
7.5.2 Mating system .....	268
7.5.3 Sexual size dimorphism .....	275
7.6 References .....	276
<b>CHAPTER 8: Summary and conclusions .....</b>	<b>283</b>

<b>APPENDIX A: An evaluation of the techniques used for the capture, immobilization, marking and habituation of the honey badger <i>Mellivora capensis</i></b> .....	291
9.1 Abstract .....	291
9.2. Introduction .....	292
9.3. Study area.....	293
9.3.1 Kgalagadi Transfrontier Park.....	293
9.3.2 Mana Pools National Park, Zimbabwe.....	293
9.4 Methods.....	294
9.4.1 Capture techniques .....	294
9.4.2 Immobilization .....	296
9.4.3. Marking .....	296
9.4.4 Age determination and classification .....	298
9.4.5 Habituation.....	301
9.5 Results & Discussion.....	302
9.5.1 Capture success .....	302
9.5.2 Immobilization .....	303
9.5.3. Marking.....	304
9.5.4. Habituation.....	306
9.6 References.....	307
APPENDIX B .....	309
APPENDIX C: .....	310
APPENDIX D .....	313

## List of Tables

<b>Table 2.1</b>	Monthly rainfall records measured at three weather stations in the KTP summarized into seasonal totals (mm) for the period of study: June 1996- Dec 1999.....	25
<b>Table 2.2</b>	Estimations of the handling time (digging time + eating time) required for the successful capture of ten common food items eaten by the honey badger (5 females; 4 males) in the southern Kalahari. There were no significant differences when using an individual honey badger as the sampling unit. Prey items are presented in order of overall profitability (g / handling time).....	36
<b>Table 2.3</b>	Seasonal differences in the diet, expressed as percentage frequency of occurrence and percentage biomass contributed by each prey category to overall diet, of the honey badger in the KTP. ....	38
<b>Table 2.4</b>	Seasonal differences in the diversity (Levins niche breadth index and Brillouin index) and species richness of the diet of honey badgers in the KTP. ....	39
<b>Table 2.5</b>	Mean and standard error of linear and mass measurements of male and female adult honey badgers in the KTP. ....	46
<b>Table 2.6</b>	Sexual differences in the diet of habituated honey badgers (five females, four males) in the KTP expressed as the percentage frequency and percentage biomass contributed by each prey category to overall diet. The niche breadth index and species richness of male and female diets are given for comparison. ....	49
<b>Table 2.7</b>	The average daily consumption of male and female honey badgers determined from continuous 24 hour observation periods and expressed as the mean (standard error) biomass of food eaten per day and the biomass ingested per kilogram of body weight per day with a direct comparison between one male and one female honey badger of known body mass. ....	52
<b>Table 2.8</b>	Comparison of consumption rate, foraging rate and digging success of male and female honey badgers in the KTP. Within each category the differences were not statistically significant when using individual honey badgers (five females; four males) as the sampling unit. Sample size (n) represents the number of observation periods used for the analysis in each category. ....	54

<b>Table 2.9</b>	Seasonal variations in consumption rate, hunting success and biomass ingested per gram of body weight of the honey badger in the KTP. ....	55
<b>Table 3.1</b>	A seasonal and sexual comparison of the percentage of the day the honey badger spends active, resting, foraging and engaged in social interactions and other activities. Percentages were calculated from whole day continuous observations only (five females; four males).....	80
<b>Table 3.2</b>	Results of significance tests (two-sided, two sample t-tests) comparing intersexual differences in the daily proportion of time spent in different activities. <sup>1</sup> .....	81
<b>Table 3.3</b>	Comparison of the types of refuge holes used by male and female honey badgers in the KTP.....	83
<b>Table 3.4</b>	A comparison of seasonal and daily differences in the length of the two active and two resting periods of the honey badger in the KTP. ....	84
<b>Table 3.5</b>	Seasonal changes in the average time of emergence and entry into the resting burrow for the two daily active periods of honey badgers in the KTP.....	89
<b>Table 3.6</b>	Comparison of the percentage of the four most common prey categories caught by honey badgers during diurnal and nocturnal foraging. The percentages were calculated from the total number of prey items caught within each prey category....	95
<b>Table 4.1</b>	Type and frequency of interspecific interactions observed between the honey badger and other mammalian carnivore species in the southern Kalahari from direct observations and from tracking spoor. Interactions are ranked in ascending order of the mass of associating species, provided by data from the literature (references in section 4.2.3.). ....	115
<b>Table 4.2</b>	Relative abundance of medium and large carnivores in the central dune area of the southern Kalahari as determined from spotlight counts in dune and river habitat and a repeated spoor transect (n = 20) of 34 km through the study area. Ranked in descending order of body mass1.....	117

<b>Table 4.3</b>	Position of prey capture by female (n = 236) and male (n = 400) honey badgers when digging for small mammals (<100 g) and small reptiles (< 100 g) in the KTP, showing the percentage of prey that escaped and were therefore potentially available for capture by associating predators and honey badger digging success when foraging alone. ....	119
<b>Table 4.4</b>	Seasonal differences in the number of hours and relative percentage of time the black-backed jackal and pale chanting-goshawks were observed with the honey badger in the KTP. The data for each season are pooled over the three years study period (1996-1999) .....	121
<b>Table 4.5</b>	Percentage of available prey items caught by the honey badger, pale chanting-goshawk and black-backed jackal when foraging in association, where prey available refers to prey items that escaped above ground while the honey badger was digging.....	123
<b>Table 4.6</b>	A comparison of the capture success (%) and intake rate (g / min) of male and female honey badgers foraging for small reptiles and small mammals in association with the black-backed jackal and pale chanting-goshawk in the KTP and when foraging alone.....	124
<b>Table 5.1</b>	Overall home range size of female and male (young & adult) honey badgers in the KTP, showing the periods of observations, and number of points. Home range area is calculated as the 100 % & 95 % MCP of all points and the 100 % MCP from only burrow positions, where sufficient points are available. ....	155
<b>Table 5.2</b>	Comparison of the dry (May – Aug) and wet season (Sep - Apr) home ranges in male and females honey badgers in the KTP. Home ranges were calculated as the 100 % MCP from resting positions for individuals where at least 30 locations were available for each season. In females, the home ranges of individuals with den cubs during that season are marked in bold (section 5.4.2).....	166
<b>Table 5.3</b>	The median rate of travel, distance moved and percentage of home range used each day in male and female honey badgers. The median (with sample sizes in brackets) rather than the mean is presented as the data have a skewed distribution and were analysed with a Mann Whitney U-test. ....	169

<b>Table 5.4</b>	Comparison of rate of travel, straight line distances and percentage of home range used per day in different age and sex categories. In all cases Mann-Whitney tests were used.....	170
<b>Table 6.1</b>	Main hypotheses and predictions related to the function of scent marking in mustelids.....	194
<b>Table 6.2</b>	Number and type of scent marking events visually recorded in male and female honey badgers in the KTP (five females; five adult males; two young males).....	198
<b>Table 6.3</b>	Visual observations of sexual and age related differences in the scent marking behaviour of the honey badger at latrines in the KTP.....	232
<b>Table 6.4</b>	Scent marking and mating activities of an adult female honey badger during 16 days of continuous visual observations. ....	234
<b>Table 6.6</b>	The position of squat-marking events in adult male (4 individuals) and adult female (5 individuals) honey badgers in the KTP.....	243
<b>Table 7.1</b>	Timing of births and independence of honey badger cubs in the KTP. In some cases date of birth was estimated from the size of the cub when it was first observed. ....	242
<b>Table 7.2</b>	Frequency and type of paired interactions and associations observed between male honey badgers in the KTP. ....	248
<b>Table 7.3</b>	Descriptions of intimidation and appeasement postures and associated vocalizations observed in and female male honey badgers during paired interactions in the KTP.....	249
<b>Table 7.4</b>	Comparison of the body mass, linear dimensions and testes area of young and adult male honey badgers with and without a scar in the KTP .....	256
<b>Table 9.1</b>	Descriptions of the age categories used in this study to assess captured honey badgers.....	299

**List of Figures**

**Figure 2.1** The relationship between percentage frequency of small mammals consumed by honey badgers and the relative abundance of small mammals estimated from rodent trapping from the cold-dry season 1997 to the hot-dry season 1999. .... 42

**Figure 2.2** Annual and seasonal changes in the proportions of small reptiles, scorpions and small mammals in the diet of honey badgers in the KTP, from visual observations . 42

**Figure 2.3** Seasonal and annual changes in the frequency of occurrence of scorpions and large reptiles in the diet of honey badgers in the KTP from visual observations. .... 43

**Figure 2.4** Seasonal and annual changes in the frequency of occurrence of tsama melons and solitary bee larvae in the diet of honey badgers in the KTP, showing the peak in the diet in the cold dry season of 1998 in both food categories. .... 43

**Figure 2.5** Seasonal and annual changes in the frequency of occurrence of large mammals and birds in the diet of honey badgers in the KTP. .... 45

**Figure 2.6** Average mass of male and female honey badger cubs of different ages captured during the study. Data on the mass increase of a female cub hand-reared in Howletts Zoo, England is also shown for comparison (adapted from Johnstone-Scott, 1975)..... 47

**Figure 3.1** Seasonal changes in the average maximum and minimum temperatures during the study period in the KTP..... 74

**Figure 3.2** Average hourly changes in temperature in the hot-wet, cold-dry and hot-dry season calculated from the nearest town, Upington (provided by the South African Weather Bureau). The arrows indicate the average time of sunrise and sunset for each season calculated from a GPS location in the centre of the study area. .... 74

- Figure 3.3** Overall sexual differences in the daily time budgets of the honey badger calculated from continuous 24 h observations of habituated individuals (Males: n = 61 days; females: n = 63 days). Social behaviour refers to latrine checking, scent marking, and intraspecific interactions while “other” refers to sand bathing, scratching, playing and short duration resting (< 30 min)..... 79
- Figure 3.4** Daily activity schedule of male and female honey badgers in the hot-wet (a), cold-dry (b) and hot-dry (c) season showing the two-peaked pattern. Data were calculated as the mean percentage of observation time that individual honey badgers were active for each hour of the day. The number of hours of observation for each hour of the day are presented in Appendix D. The arrows indicate sunrise and sunset for midpoints of the season..... 86
- Figure 3.5** Seasonal differences in the relative nocturnal and diurnal activity of honey badgers in the KTP. To account for different amounts of observation time during the day and night, the time spent active was calculated as a percentage of the amount of time a honey badger were observed in each period (day or night) in each season. .... 89
- Figure 3.6** The frequency of sand bathing events in honey badgers in the KTP and hourly changes in maximum temperature in the cold-dry and hot-wet season. Sand bathing frequency was calculated as the number of sand bathing events observed per hour of activity recorded for that hour of the day ..... 92
- Figure 3.7** Relationship between average maximum temperature and the percentage of time honey badgers rest in a burrow during daylight hours showing the increase in burrow use with increasing temperature..... 93
- Figure 3.8** Two-hourly changes in the rate of capture (captures/ hour of foraging) of four common prey species; three rodents (*G. paeba*, *T. brantsii*, *R. pumilio*) and one reptile (*P. garrulous*) by honey badgers in the KTP. .... 96

- Figure 4.1** Percentage of time black-backed jackals were observed with honey badgers relative to the number of hours honey badgers were observed foraging during each hour of the day, averaged over the study period (1996-1999) ..... 127
- Figure 5.1** Incremental area analysis of two habituated male honey badgers showing the change in the range area as successive burrow positions were collected. Am 4 home range size = 640 km<sup>2</sup>, n = 104 resting positions; Am12 home range size = 625 km<sup>2</sup>; n = 107 resting positions. .... 158
- Figure 5.2** Incremental area analysis of two habituated female honey badgers showing the change in the range area as successive burrow positions were collected. Am38 home range size = 81 km<sup>2</sup>, n = 124 resting positions; Af16 home range size = 167 km<sup>2</sup>; n = 123 resting positions. .... 160
- Figure 5.3** Minimum convex polygons (100 %) of nine radio-marked scar-back male honey badgers and the spot positions of three unmarked, scarback males. More than 30 locations were available for the three individuals shown in bold (Am 12, Am 43, Am 9), with less than 30 positions for the other six individuals. .... 160
- Figure 5.4** Minimum convex polygons (100 %) of two adult male honey badgers without back scars (Am 24, Am 4) and one scarback male (Am 12), showing the overlap in space use. .... 161
- Figure 5.5** Minimum convex polygons (100 %) enclosing all positions of three young males (Am 11, Am 36, Am 14) and one adult scarback male (Am 12). The natal home range of Am14 when he was still dependent on his mother (Af15) is also shown by the dotted line. .... 161
- Figure 5.6** Home range outlines (100 % minimum convex polygons of all points) of ten radio-marked female honey badgers showing the range overlap and size of female home ranges in relation to an adult scarback male honey badger (Am12) utilizing the same area. The positions of three unmarked females within the study area are also shown to provide an indication of the density of female honey badgers. .... 163

- Figure 5.7** Percentage overlap in neighbouring female home ranges from peeled polygons of 40 % ( $\bar{x}$  = 13 % overlap, 5 overlappers) 60 % ( $\bar{x}$  = 18.2 %, 16 overlappers), 90 % ( $\bar{x}$  = 28 %, 25 overlappers) & 95 % ( $\bar{x}$  = 25 %, 30 overlappers)..... 164
- Figure 5.8** Increase in the size of a young male's home range over a 20 month period (100 % MCP of all points; Am 4), showing the initial relatively small home range for 11 months followed by a rapid expansion and shift in home range area. The home range of an adult scarback male (Am12; dominant male in the area; Chapter 7) is also shown for comparison..... 167
- Figure 5.9** Five day tracks of an adult male scar-back honey badger during different months of the year over a 15 month period ..... 171
- Figure 5.10** Five day tracks of an adult female (Af 16) with a female cub (Jf10) when the cub was 9 (a), 12 (b), and 15 (c) months old respectively. During the period 03/98 (c) the female was pregnant and the cub dispersed three weeks later when the next cub (J♂27) was born. Tracks are generated from continuous visual observations where GPS points were taken for each change in behaviour or at 10-minute intervals. .... 172
- Figure 5.11** Five-day tracks of an adult female during oestrus and pregnancy (no cub) and with den cubs of different ages within her home range, where black dots represent den sites. No data were available for this female with a foraging cub (>3 months old). Tracks are generated from continuous visual observations where GPS points were taken for each change in behaviour or at 10-minute intervals..... 173
- Figure 5.12** Comparison of the average home range area in nine medium sized mustelids (> 5 kg) showing the relatively large home range of the honey badger and the wolverine *Gulo gulo*. All data except for the honey badger from Johnson et al (2000). .... 176
- Figure 6.1** The position of honey badger latrines relative to possible landmarks in the KTP showing (a) all the latrines described (n = 122), (b) long term latrines (n = 37).and (c) temporary defaecation sites (n = 32)..... 200

- Figure 6.2** Proportion of known honey badger latrines active (scats and/or spoor) during each month of the year for two years in the KTP. Note that there appears to be no seasonal peak in latrine use. .... 202
- Figure 6.3** Monthly level of activity at two honey badger latrines (1 & 4) for the period September 1996 – December 1999 in the KTP. Note the variation in latrine activity both within and between the two latrines. Activity was scored from 0-3 based on the number of visits in that month where 3 =  $\geq 10$  visits, 2 = 5 - 9 visits, 1 =  $< 5$  visits and 0 = no visits. .... 203
- Figure 6.4** The rate of latrine visits in adult female (723 h obs; 5 individuals), adult male (636 h; 4 individuals) and young male (309 h; 2 individuals) honey badgers in the KTP. Kruskal-Wallis test  $H(2, n = 11) = 8.33; p < 0.05$  (young males vs. adult males,  $Q = 2.96, p < 0.05$ ; females vs. adult males  $Q = 2.43, p < 0.05$ ; females vs. young males, not significant; Zar, 1999). .... 205
- Figure 6.5** The timing of visits to latrines in three habituated female honey badgers over their individual periods of direct observation. Observations of mating, birth of cubs and cub independence are shown to illustrate the association between female latrine visits and reproductive behaviour. .... 207
- Figure 6.6** Spatial distribution of latrines and scent marking sites within the minimum convex polygon home range outline of an adult male honey badger (Am12). Note the hinterland distribution of latrines and scent marking sites. .... 212
- Figure 6.7** Rate of token urination in adult female ( $n = 5$ ) and young male ( $n = 2$ ) honey badgers in the KTP (Mann-Whitney U test,  $Z = -1.936; p = 0.05$ ). Adult males were not observed to use token urination. Only data from visual observations of habituated individuals was used for this analysis. .... 213
- Figure 6.8:** Scent marking positions of two adult female honey badgers (Af38, Af16) within their home ranges ( $105 \text{ km}^2, 179.7 \text{ km}^2$  respectively). Both the positions of latrines visited by females as well as token urination sites along the foraging paths are indicated. .... 215

- Figure 6.9** Rate of squat marking in adult female (n = 5), young male (n = 2) and adult male (n = 4) honey badgers in the KTP (no significant differences). Only data from visual observations of habituated individuals was used for this analysis..... 216
- Figure 7.1** Paired aggressive, agonistic and amicable interactions observed between known male honey badgers of different age classes in the KTP. The arrows move from a dominant to a subordinate individual ..... 253
- Figure 7.2** Relationship between male honey badger mass, testes area and age category, showing the increase in testes size after independence associated with a change from the young to adult male age category. Scar back males could not be distinguished from non scarbacks on the basis of testes area or mass. .... 255
- Figure 7.3** A comparison of the average length of gestation in ten medium sized mustelids (> 5 kg) with the closed circles representing those species that show delayed implantation. The length of the delay (in days) is represented by the number next to name. All data, except for the honey badger, are from Johnson *et al.* (2000)..... 262
- Figure 7.4** A comparison of the litter sizes of ten medium sized mustelid species (adult female mass is > 5 kg) showing the unusually smaller litter sizes of the honey badger, smooth coated otter *Lutrogale perspicillata* and sea otter *Enhydra lutris*. All data except for the honey badger are from Johnson *et al.* (2000). .... 263

## List of Plates 1-

- Plate 7.1** Wounds on an adult scarback male (Am13) caught while interacting with other adult males around an oestrous females.....245
- Plate 7.2** Prominent scar in the middle of the back of an adult male honey badger (Am 9). The area of thickening measured 13.6 cm x 15 cm with an inner area of white hair.....245
- Plate 9.1** The teeth (primarily canines and incisors) of honey badgers from three age classes, based on tooth eruption and wear from the KTP. Note the wear on the third incisor on the upper jaw. The worn incisors and canines of two individuals (Plate 9.1 E and 9.1F) that were considered old are also shown .....300