- Chapter 5 -

Spatial organisation of the honey badger *Mellivora capensis* in the southern Kalahari: factors affecting home range size and movement patterns.

5.1 Abstract

Radio-tracking locations of 25 individuals (13 females; 12 males) and visual observations of nine habituated individuals were used to investigate the spatial organisation and movement patterns of the honey badger *Mellivora capensis* in the southern Kalahari. The home ranges of adult male honey badgers (548 km^2) are significantly larger than the home ranges of adult females (138 km^2). Female home range size was five times larger than predicted with a mean percentage overlap of 25 % between neighbouring females. The extensive home ranges of females appear to be a function of low prey availability and the long period of cub dependence (12-16 months). While females do not defend a territory, home ranges centers are more regularly spaced than expected and females avoid each other temporally suggesting a loose territorial system. In contrast, males do not support the typical mustelid pattern of intrasexual territoriality but instead have a system of overlapping home ranges that encompass the home ranges of up to 13 females. Males and females differ significantly in their rate of travel (3.7 km/h vs. 2.1 km/h), straight line (4.6 km vs. 1.8 km) and actual distance (13.7 km vs. 7.5 km) moved during an active period but do not differ in the percentage of their home range area traversed in a single day (3 %). Young males have smaller home ranges (178 km^2) and move slower and shorter distances than adult males, and show a spacing pattern more similar to adult females than adult males with food the limiting resource. In common with other solitary mustelids, the spatial organisation suggests a polygynous mating system.

5.2 Introduction

Spatial organisation describes the manner in which conspecifics within a population distribute themselves on a landscape, including the maintenance of core areas, home ranges and territories (Mares & Lacher, 1987). Not only is knowledge of the spatial organisation important for understanding the mating system of a species, but also for formulating conservation management strategies, as it relates to issues of effective population size, population persistence, genetic diversity, reserve size and the effect of interventions (Caro & Durant, 1994; Komdeur & Deerenberg, 1997).

In the Mustelidae, a spacing pattern of intra-sexual territoriality with a polygynous mating system appears to be characteristic, although the family also includes several social species including the group living European badger *Meles meles* and four otter species (Powell, 1979; Moors, 1980; Sandell, 1989; Balharry, 1993; Clevenger, 1993; Johnson *et al.*, 2000). The honey badger *Mellivora capensis* is a relatively large mustelid (6-14 kg) that has not been well studied despite its extensive distribution across the greater part of Africa south of the Sahara and extending through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula (Neal, 1990; F. Cuzin, *in litt.*, 2001).

The aim of this chapter is to describe the spatial organisation of free-living honey badgers in the southern Kalahari and to investigate factors affecting the home range size and movement patterns of male and female honey badgers. As part of this study it has been shown that the honey badger is a solitary forager with a wide, largely carnivorous diet (Chapter 2), but little is known of its spatial requirements or movement patterns. In carnivores, it has repeatedly been shown that home range size appears to scale allometrically with body mass, but at a greater rate than expected from basal metabolic rate or daily metabolic needs (Reiss, 1988). A variety of power functions of body mass have been derived to predict home range area in carnivores (McNab, 1963; Gittleman & Harvey, 1982; Harestad & Bunnell, 1979; Lindstedt *et al.*, 1986; Swihart *et al.*, 1988) and more recently in mustelids in particular (Johnson *et al.*, 2000). Since the honey badger shows marked sexual size dimorphism with males at least a third larger than females, it is predicted that males will have larger home ranges than females based on metabolic considerations alone.

It is generally agreed that in solitary carnivores, including most mustelids, female spacing patterns are primarily determined by the abundance and dispersion of food while male spacing patterns are primarily influenced by the availability and dispersion of receptive females, at least during the breeding season (Powell, 1979; Erlinge & Sandell, 1986; Sandell, 1989; Johnson *et al.*, 2000). This model of sexual differences in reproductive strategies has also been supported in many other taxa (Trivers, 1972; Emlen & Oring, 1977). Theory predicts that if the limiting resource is predictable in space and time and is concentrated within a restricted area, it can be defended and the development of territorial behaviour is favoured (Brown & Orians, 1970; Hixon, 1980), whereas a system of overlapping ranges is likely when the timing and spacing of the resource varies (Erlinge & Sandell, 1986; Sandell, 1989).

For an adult female honey badger it is therefore expected that the home range size should be just large enough to include sufficient food to meet her energetic requirements (Goodrich & Buskirk, 1998). Since the dry season (May –Aug) is the lean season for the honey badger in the KTP, with decreased consumption rates and increased foraging time (Chapter 2), it is predicted that female honey badgers will show seasonal changes in home range use and movement patterns. Further to this, if receptive females, rather than food are the limiting resource for male honey badgers, then the home ranges of adult males should be larger than predicted based on metabolic demands alone (Goodrich & Buskirk, 1998) and there should be no seasonal changes in home range size since breeding appears to be asynchronous in the southern Kalahari and receptive females are available throughout the year (Minta 1993; Goodrich & Buskirk, 1998; Chapter 7).

5.3 Study area and methods

5.3.1 Study Area

The study was initiated in July 1996 and continued until December 1999 (42 months) in the Kgalagadi Transfrontier Park (KTP), which encompasses an area of 36 200 km^2 with the Kalahari Gemsbok National Park, South Africa (KGNP)and neighbouring Gemsbok National Park, Botswana. It is a semi desert region and the vegetation is described by Acocks (1988) as the western form of Kalahari thornveld with a very open savanna of *Acacia haemotoxylon* and *Acacia erioloba* with desert grasses. This study was primarily conducted in the central dune area of the KGNP, which is characterized by medium to high dunes on reddish sands where *A. haemotoxylon* appears in a shrublike form with scattered *Boscia albitrunca* trees (Van Rooyen *et al.*, 1984).

The study area falls between the 200 mm and 250 mm isohyets and is characterized by low, irregular annual rainfall (Mills & Retief, 1984). The variability of the rainfall plays a major role in the vegetation of the KTP (Leistner, 1967), and large differences in floristic composition, basal cover and density can be expected in the short and medium term (Van Rooyen, 1984). For the purposes of this study, two seasons are distinguished, the wet season from Sep - Apr when the mean monthly temperature is approximately 20°C or higher and the majority of rain falls and the dry season from May-Aug when the mean monthly temperature is below 20°C and rainfall is rare (Mills & Retief, 1984).

5.3.2 Data collection

Honey badger spoor was located by a Khumani-San tracker and tracked on foot until the individual could be ambushed and caught in a hand net where it was hand injected and immobilized with Zoletil (Appendix A). Thirteen females, 17 males and 13 cubs were caught and 25 individuals (13 females, 12 males) were radio-marked with Telonics radio-collars (Appendix A). A wildlife veterinarian subsequently implanted ten of the radio-marked adults (five females and five males), and three cubs (one male, two females) with radio implants (Appendix A). As it was not possible to recognize individuals by pelage variations alone, cubs that were captured with their mothers and all adults that were captured but not radio-marked were freeze branded (Histofreezer; Appendix A) with a unique mark on the upper shoulder or thigh within an area of black hair. Since hair grew back white after freeze-branding, the freeze-brands were visible with binoculars. The techniques of capture, radio marking, freeze-branding and habituation are presented in detail in Appendix A.

The mass and linear dimensions (body length, shoulder height, neck circumference, testes) of all captured animals were measured (Chapter 2). Honey badgers were divided into four broad age categories based on tooth wear, behaviour, body size, and condition i.e. den cub (0-3 months), foraging cub (3 months to independence), young adult (age 1-3 yrs) and adult (older than three years). Adult males were further divided into males with a prominent back scar and those without a back scar. Since the scar is thought to develop with age from male-male contests (Chapter 7), scarback males are considered older than non scarbacks. These age classes are presented in detail in Appendix A.

Radio-marked honey badgers were located from the air and the ground. The radio-marked honey badgers were found from the air at least once a month during the first 2.5 years (June

1996 - Dec 1998), and this was later increased to once every two weeks for the final year of field work (1999). The geographic co-ordinates (latitude and longitude) of each honey badger were recorded using a GPS and were found to be accurate within 500 m or less of the actual position of the animal when relocated from the ground within a few hours. Locations collected during a single three-hour flight were considered to be simultaneous and used to analyse the linear distance between neighbouring individuals at the same time.

Ground tracking was also used to locate honey badgers on an opportunistic basis as often as possible. A two element antenna on a 2 m pole was attached to the vehicle i.e. 3.5 m above the ground, and this could be extended to 6 m. A signal could be heard from a maximum distance of 5 km but signal strength was greatly reduced (< 2 km) when a honey badger was in a burrow. Radio implants were less powerful with a mean signal strength of < 2 km. Due to the difficulties in finding honey badgers from the ground, particularly the males, positions were obtained irregularly. As a result several home ranges were calculated on the basis of small sample sizes and should be regarded as minimum ranges. These data are included as no previous data on population densities are available for honey badgers and these data are important for assessing home range overlap.

Nine radio-marked adult badgers (five females with five cubs and four males) were habituated to the vehicle, and direct continuous observations of these individuals, ranging from one to twelve days ($\bar{x} = 4$ days, n = 91) with an additional 57 short observation periods (less than 24 h) ranging from 45 min to 20 h (5811 h in total) were made. At the start and end of each activity period the GPS position of the individuals and odometer reading on the vehicle were noted. GPS positions were also taken at each change in behaviour or alternatively at 10 min intervals if the behaviour did not change. This enabled calculation of the rate of travel, and straight line and actual distances travelled.

5.3.2 Data analysis

Animal location data were analysed using the computer program "Ranges V" (Kenward, 1991). Collection and analysis of radio-tracking data is the subject of ongoing review (Anderson, 1982; Harris *et al.*, 1990). For this study, home range area and overlap were evaluated using minimum convex polygons (MCP; Mohr, 1947) to enable comparison with studies of other mustelids (Harris *et al.*, 1990; Balharry, 1993). This technique is considered a relatively robust, non-parametric interpretation of home range size where more than 30 points are available, although it is sensitive to outliers (Swihart & Slade, 1985; Kenward, 1987; Balharry, 1993). To minimize the effect of outliers, both the 100 % and the peeled 95 % MCP for all points were calculated. The 95 % MCP excludes 5 % of the fixes furthest from the range centre calculated as the harmonic mean fix (Kenward, 1987; Kenward, 1991). Similarly, the mean percentage of overlap between peeled polygons of 30, 60 and 90 % from home ranges of neighbouring females were used to examine the core area of an adult female's home range i.e. an exclusive area with < 10 % overlap with neighbouring females (Sandell, 1989).

Points from continuous observations of habituated individuals are autocorrelated, but using only statistically independent points (Swihart & Slade, 1985) would have resulted in too few points being available for home range analysis and the loss of valuable behavioural data (Minta, 1993). To assess the effect of autocorrelation, the 100 % MCP of only resting positions for each individual were also calculated. Honey badgers do not have a fixed den site but rest in a different place each day. Resting positions can therefore be considered biologically independent as serial locations are separated by a major activity shift and the mean straight line distance moved between resting positions was 4.6 km (range 1 – 17 km) for males and 2.8 km (range 1 – 9 km) for females (Lair, 1987; Minta, 1993). Nearest neighbour analysis of range centre spacing, the degree of overlap (Ranges V) between neighbours and linear distances between simultaneous locations of neighbouring females from aerial tracking points (within three hours) were used to analyse spacing between adult females.

Statistical analysis of sexual and seasonal differences in home range size and movement patterns were made using non-parametric Mann-Whitney U test and Kruskal-Wallis test (Statistica: Stasoft, 1995). Seasonal differences in the mean percentage of home range overlap were arcsine transformed to achieve normality and means were compared with the two-sample, two sided Student's t-tests. All statistical tests follow Zar (1999).

5.4 Results

5.4.1 Home range

Sufficient data for home range analysis (> 30 points; Kenward, 1991) were obtained from 21 radio-marked honey badgers when all points were used (ten adult females; four young males, seven adult males; Table 5.1) and 10 individuals when only resting positions were used (five females; one young male and four adult males; Table 5.1). The home range areas calculated from 100 % and 95 % minimum convex polygons of all points and 100 % MCP of only resting positions did not differ significantly (Kruskal-Wallis). The results are presented for all methods for comparison with other studies. No data were collected on home ranges of young females, as all the females captured were adults.

Within adult males the size of the home range (100 % MCP) is significantly positively correlated to the number of points collected ($r = 0.78$, $p < 0.01$, $n = 7$), and there is a large variation in home range from 229 km^2 – 844 km^2.

Table 5.1 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.

Id No and age (H=habituated)	100 % MCP (km^2)	95 % MCP (km^2)	No. Points	Burrow MCP (km^2)	No. Points	Months followed
A. Adult females						
♀20 (H)	83	52	302	79	75	20
♀17	96	84	381	-	-	7
♀15	102	53	87	-	-	6
♀38 (H)	105	99	1326	81	124	12
♀34	135	81	52	-	-	15
♀30	137	97	161	-	-	18
♀25 (H)	151	117	186	148	131	17
♀31	177	166	47	-	-	11
♀16 (H)	201	163	911	167	123	17
♀07 (H)	205	197	413	160	77	17
Overall $\overline{x}$ (S.E)	*139.2 ± 14*	*111 ± 16*		*129 ± 20*		
B. Young males						
♂14	82	75	87	-	-	6
♂36	110	79	32	-	-	4
♂11	323	161	85	-	-	11
♂04[1] (H)	236	221	931	186	195	8
Overall $\overline{x}$ ± (S.E)	*187.8 ± 56*	*134 ± 35*		*186*		
C. Adult males						
♂05-scarback	229	130	121	-	-	6
♂06-scarback	335	314	106	-	-	3
♂09-scarback	403	260	466	-	-	15
♂43-scarback (H)	588	346	311	472	44	7
♂04 (H)	664	625	778	525	70	10
♂24 (H)	776	729	261	575	73	8
♂12 scarback (H)	844	672	1671	722	107	24
Overall $\overline{x}$ (S.E)	*548 ± 88*	*439 ± 88*		*573 ± 54*		

[1] = Moved from young male to adult male with associated increase in testes size and development of a back scar during study

In females there is no significant correlation between home range size and number of points collected, but the variation in home range is also relatively large ranging from 83 km^2 – 205 km^2. To investigate this further, observation curves for two habituated females and two habituated males were calculated using the increase in home range area with increasing burrow positions (Figure 5.1, Figure 5.2). The results show that both male home ranges continued to increase in size during the study and did not reach an asymptote (i.e. less than 10 % increase over 10 radio locations; Clevenger, 1993), despite the fact that more than 100 resting positions had been collected in each case (Figure 5.1). The lack of an asymptote in the size of the home ranges of adult male honey badgers suggests that they might not have a fixed home range but may rather be nomadic (Kruuk, 1995).

In females an asymptote was reached at 55 burrow positions in Af16, and initially at 50 points in Af38 with another sharp increase at 80 burrow positions which probably reflects a change in accompanying cub age (Figure 5.2). Clearly, in females at least 50 resting burrows are needed to provide an estimate of home range. There was no significant difference in the average amount of food (in grams) caught per km travelled by each adult female and no significant correlation (Spearman's rank correlation) between intake / km travelled and home range area. It is therefore considered unlikely that the large differences in female home range size are due to differences in prey availability. These differences are more likely to be the effect of unequal sampling in different seasons and in females with different aged cubs (section 5.4.2).

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 ^{2}, n =104 resting positions; Am12 home range size = 625 km ^{2}; n = 107 resting positions.

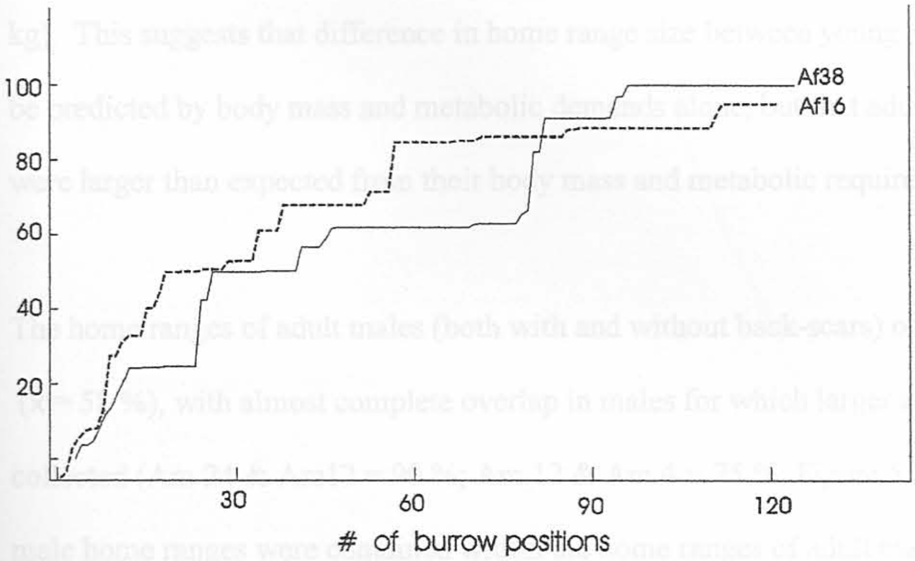


Figure 5.2 Incremental area analysis of two habituated female honey badgers showing the change in the range area as successive burrow positions were collected. Am38 home range size = 81 km^2, n = 124 resting positions; Af16 home range size = 167 km^2; n = 123 resting positions.

As predicted the overall home ranges (100 % MCP) of adult male honey badgers are significantly larger than those of adult females, (females: 139 km^2 vs. males; 548 km^2; Mann-Whitney test, $Z = -3.42$, $p < 0.01$). In addition, the results suggest that young males have significantly smaller home ranges than adult males (188 km^2; Mann-Whitney test, $Z = -2.26$, $p < 0.05$), although sufficient data were only obtained for four young males.

To test the prediction that the differences between the home range sizes of males and females is larger than predicted from differences in body size and metabolic needs alone, female home ranges are assumed to be set by metabolic demands ($HR_{♀}$) and male home ranges are predicted as $HR_{♀}$ x $M_{♂} / M_{♀}$, where M is average mass (Lindstedt *et al.*, 1986). The measured home range size of adult males is 2.5 times greater than predicted (213 km^2; $\bar{x}$ female mass = 6.2 kg; $\bar{x}$ adult male mass = 9.5 kg), but the home range size of young males is not different from the prediction (188 km^2; $\bar{x}$ female mass = 6.2 kg; $\bar{x}$ young male mass = 8.4 kg). This suggests that difference in home range size between young males and females can be predicted by body mass and metabolic demands alone, but that adult male home ranges were larger than expected from their body mass and metabolic requirements alone.

The home ranges of adult males (both with and without back-scars) overlapped extensively ($\bar{x}$ = 58 %), with almost complete overlap in males for which larger amounts of data were collected (Am 24 & Am12 = 90 %; Am 12 & Am 4 = 75 %; Figure 5.3 & Figure 5.4). Young male home ranges were contained within the home ranges of adult males (Figure 5.5). There is no evidence that either adult or young males are territorial i.e. actively excluded competitors from a specific resources or resources within a fixed space (Mares & Lacher, 1987).

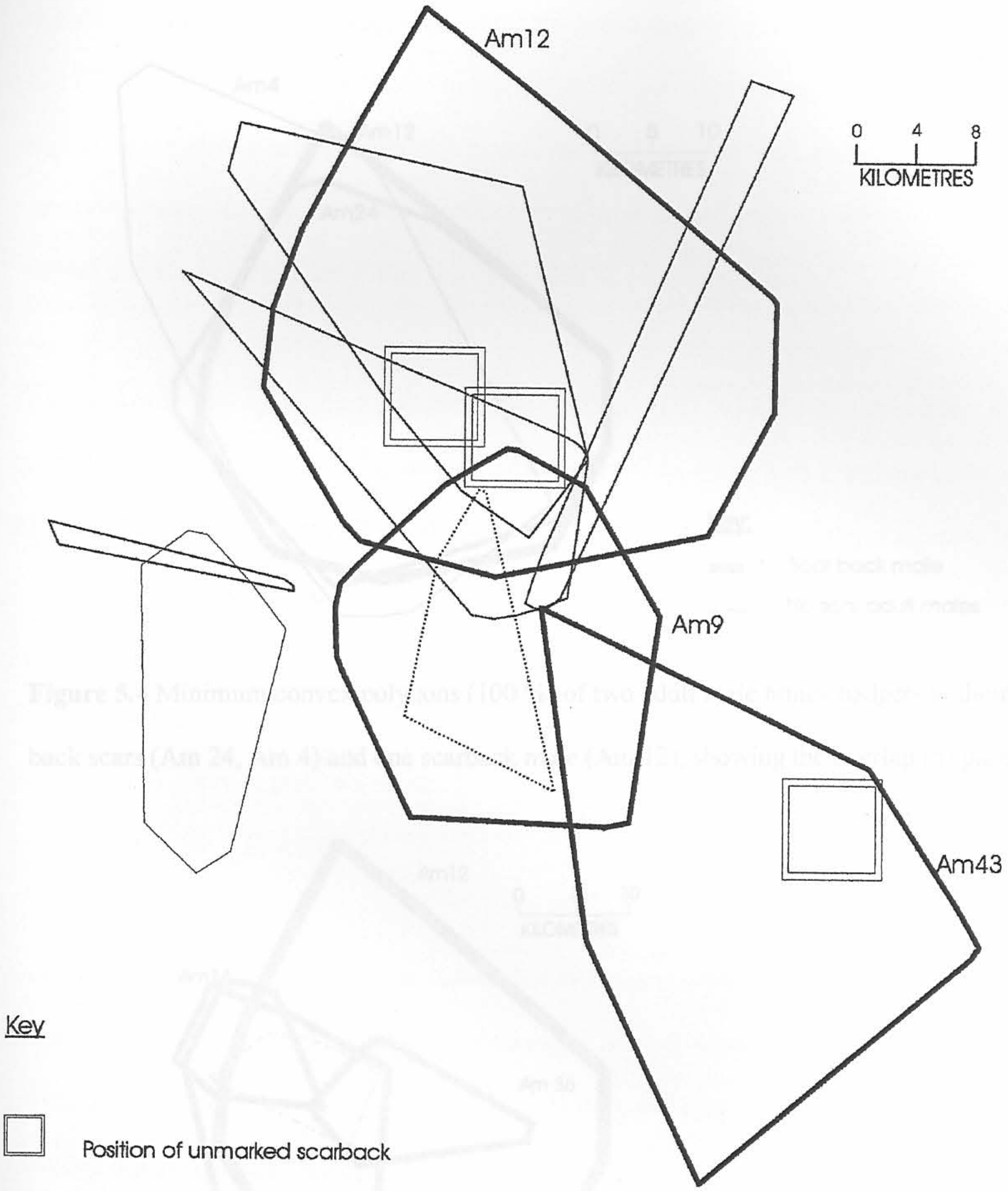


Figure 5.3 Minimum convex polygons (100 %) of nine radio-marked scar-back male honey badgers and the spot positions of three unmarked, scarback males. More than 30 locations were available for the three individuals shown in bold (Am12, Am 43, Am 9), with less than 30 positions for the other six individuals.

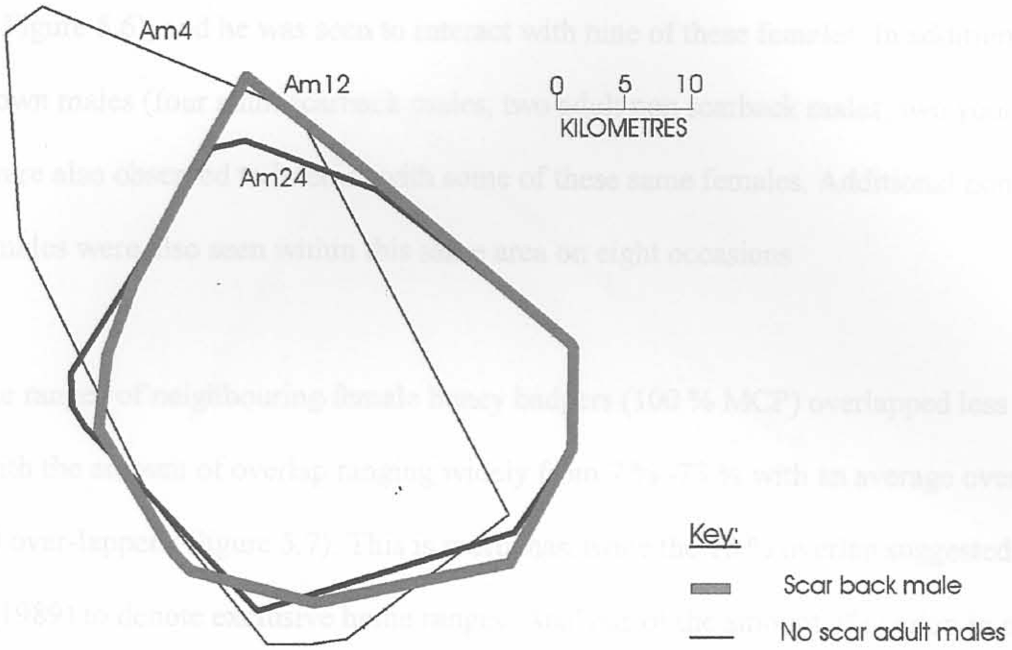


Figure 5.4 Minimum convex polygons (100 %) of two adult male honey badgers without back scars (Am 24, Am 4) and one scarback male (Am 12), showing the overlap in space use.

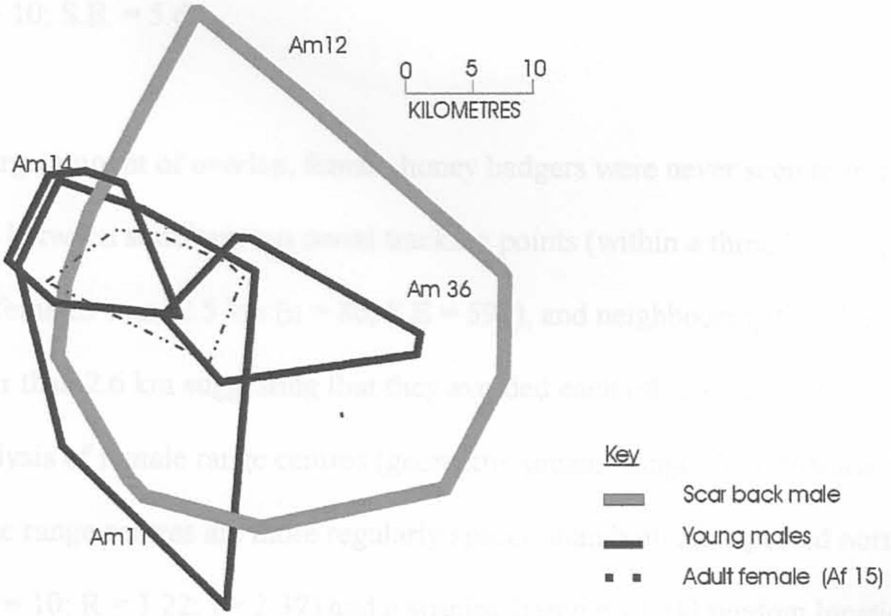


Figure 5.5 Minimum convex polygons (100 %) enclosing all positions of three young males (Am 11, Am3 6, Am 14) and one adult scarback male (Am 12). The natal home range of Am14 when he was still dependent on his mother (Af15) is also shown by the dotted line.

At least 13 females were encompassed within the home range of a single adult scar-back male (Am 12; Figure 5.6), and he was seen to interact with nine of these females. In addition, eight other known males (four adult scarback males, two adult non scarback males; two young males) were also observed to interact with some of these same females. Additional non radio-marked males were also seen within this same area on eight occasions

The home ranges of neighbouring female honey badgers (100 % MCP) overlapped less than males, with the amount of overlap ranging widely from 7 % -73 % with an average overlap of 25 % (40 over-lappers; Figure 5.7). This is more than twice the 10 % overlap suggested by Sandell (1989) to denote exclusive home ranges. Analysis of the amount of overlap in peeled polygons of 40, 60 and 90 % (section 5.3.2) showed that only the 40 % MCP showed an exclusive area for each female close to 10 % (Figure 5.7). The 40 % polygon can be therefore be considered the core area of a female honey badger's home range and it has an average area of 26 km^2 (n = 10; S.E. = 5.6).

Despite this large amount of overlap, female honey badgers were never seen to interact. The mean distance between simultaneous aerial tracking points (within a three hour flight) of neighbouring females was 12.5 km (n = 80, S.E = 599), and neighbouring females were never recorded closer than 2.6 km suggesting that they avoided each other temporally. Nearest neighbour analysis of female range centres (geometric mean; Ranges V; Kenward, 1991) showed that the range centres are more regularly spaced than both an expected normal distribution (n = 10; R = 1.22; t = 2.37) and a spacing based on 1000 random locations (n = 10; R = 1.35; t = 3.32).

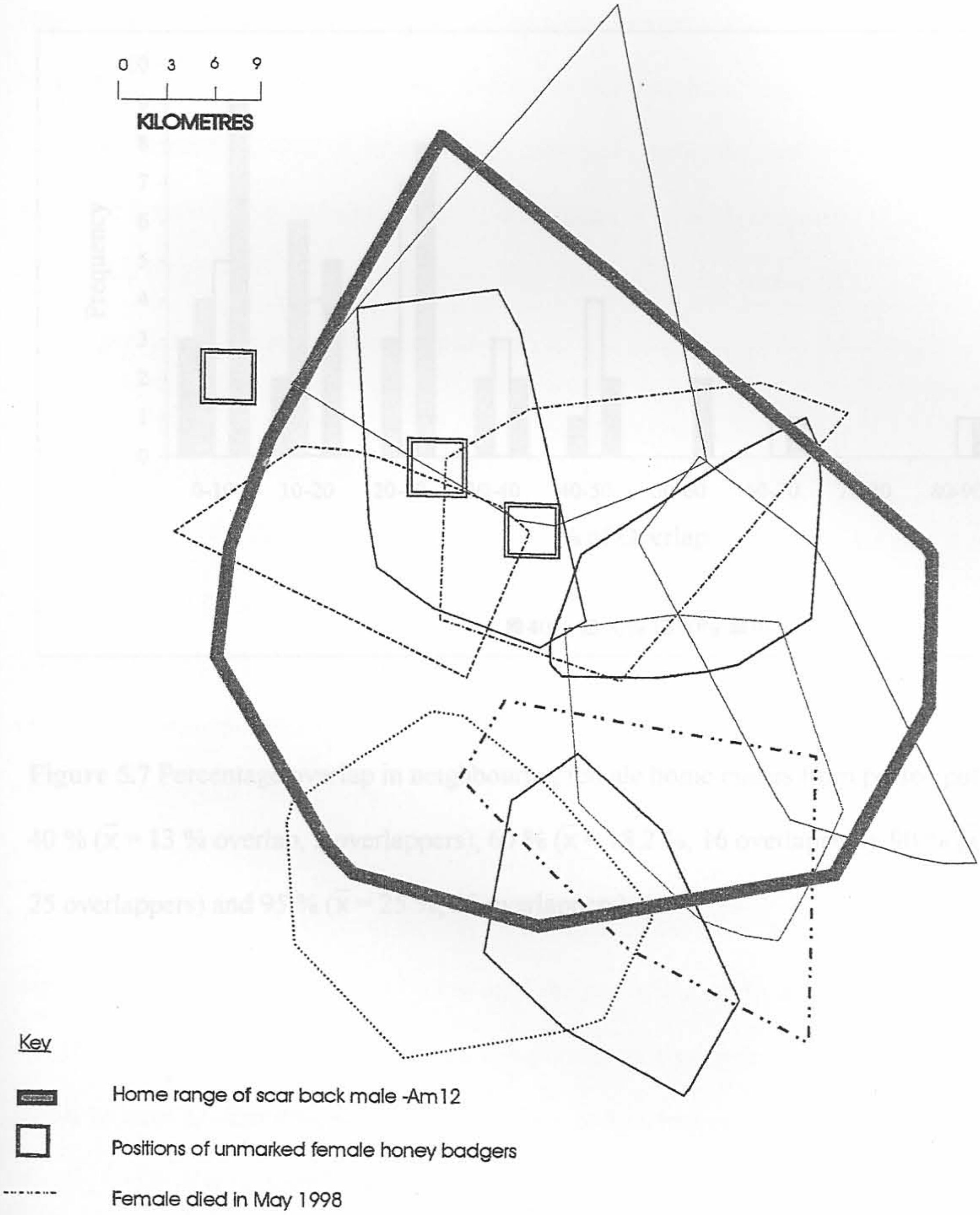


Figure 5.6 Home range outlines (100 % minimum convex polygons of all points) of ten radio-marked female honey badgers showing the range overlap and size of female home ranges in relation to an adult scarback male honey badger (Am12) utilizing the same area. The positions of three unmarked females within the study area are also shown to provide an indication of the density of female honey badgers.

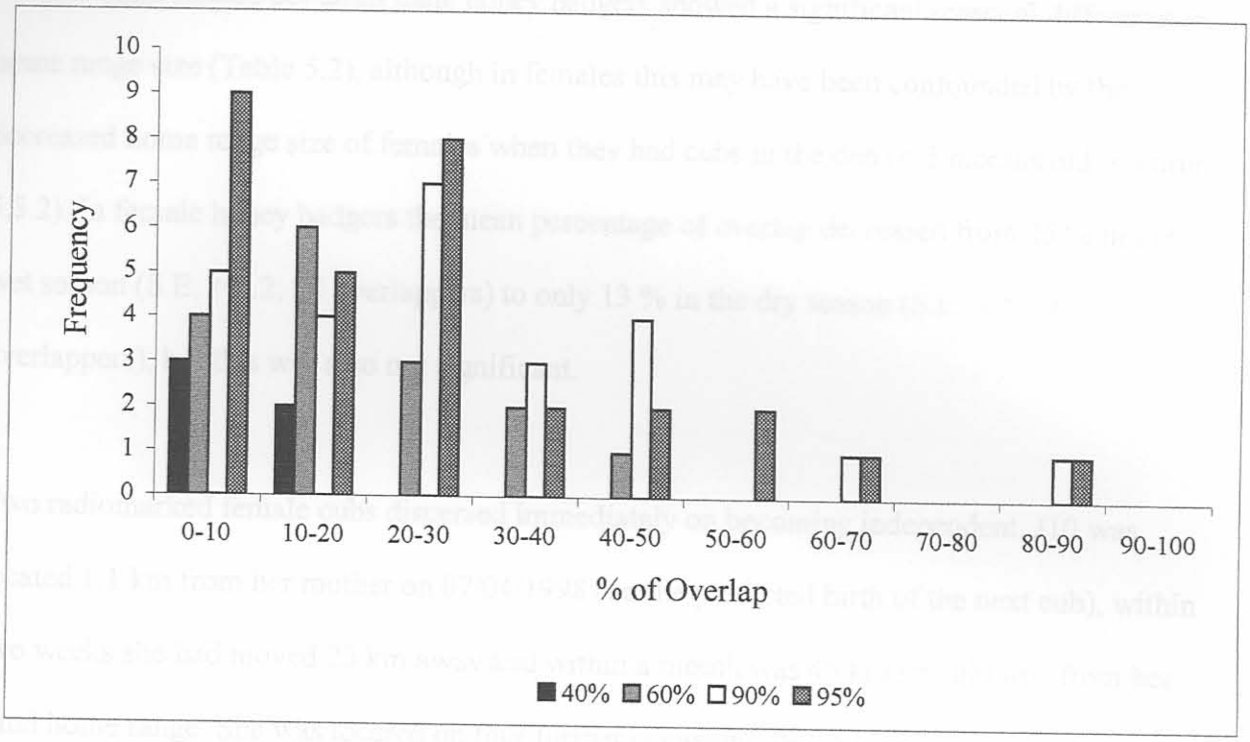


Figure 5.7 Percentage overlap in neighbouring female home ranges from peeled polygons of 40 % ($\overline{x}$ = 13 % overlap, 5 overlappers), 60 % ($\overline{x}$ = 18.2 %, 16 overlappers), 90 % ($\overline{x}$ = 28 %, 25 overlappers) and 95 % ($\overline{x}$ = 25 %, 30 overlappers).

Neither adult female nor adult male honey badgers showed a significant seasonal difference in home range size (Table 5.2), although in females this may have been confounded by the decreased home range size of females when they had cubs in the den (< 3 months old; section 5.3.2). In female honey badgers the mean percentage of overlap decreased from 25 % in the wet season (S.E. = 3.2; 25 overlappers) to only 13 % in the dry season (S.E. 3.2; 14 overlappers), but this was also not significant.

Two radiomarked female cubs dispersed immediately on becoming independent. J10 was located 1.1 km from her mother on 07/04/1998 (on the predicted birth of the next cub), within two weeks she had moved 23 km away and within a month was 45 km straight line from her natal home range. She was located on four further occasions 49 – 53 km away until contact was lost five months after dispersal (September 1998). In contrast, male cubs remained within or close to their natal home range for at least several months after independence (n = 3, Am 14, Am 33, Am11; see Figure 5.5 for the independent and natal home range of Am 14). Am 33 became independent at approximately 16 months old but after two months alone he re-joined his mother and remained with her until the end of the study, by which time he was more than two years old. Despite at least two periods of mating and courtship she did not appear to have another cub. A young male honey badger regularly followed for 20 months initially had a relatively small home range (Am4; 256 km^2; n = 1509 points; 96/08/11 – 97/04/30) but was then observed to extend his home range into a new area (560 km^2; n = 412 97/05/01 – 98/04/08; Figure 5.8). During this increase in home range area, it was observed that he was developing a small back scar and he was also observed to kill the young cub of a female (possible infanticide; Chapter 7, section 7.4.2).

Table 5.2 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 cubs in the den (< 3 months old) are marked in bold (section 5.4.2).

Id No. and sex	Home range size 100 % MCP (# locations)	
	Dry season (May –Aug)	Wet season (Sep – Apr)
Females		
Af34	96 (30)	104 (33)
Af38	**64 (52)**	**63 (83)**
Af25	103 (31)	100 (127)
Af16	**53 (43)**	138 (44)
Af07 [1]	123 (34)	159 (53)
Overall ± S.E	*88 ± 13*	*113 ± 17*
Males		
Am12	605 (76)	552 (51)
Am24	467 (35)	412 (38)
Am09	203 (42)	223 (35)
Am04	341 (35)	624 (162)
Overall ± S.E	*466 ± 93*	*453 ± 88*

[1] This female was never observed to have a cub

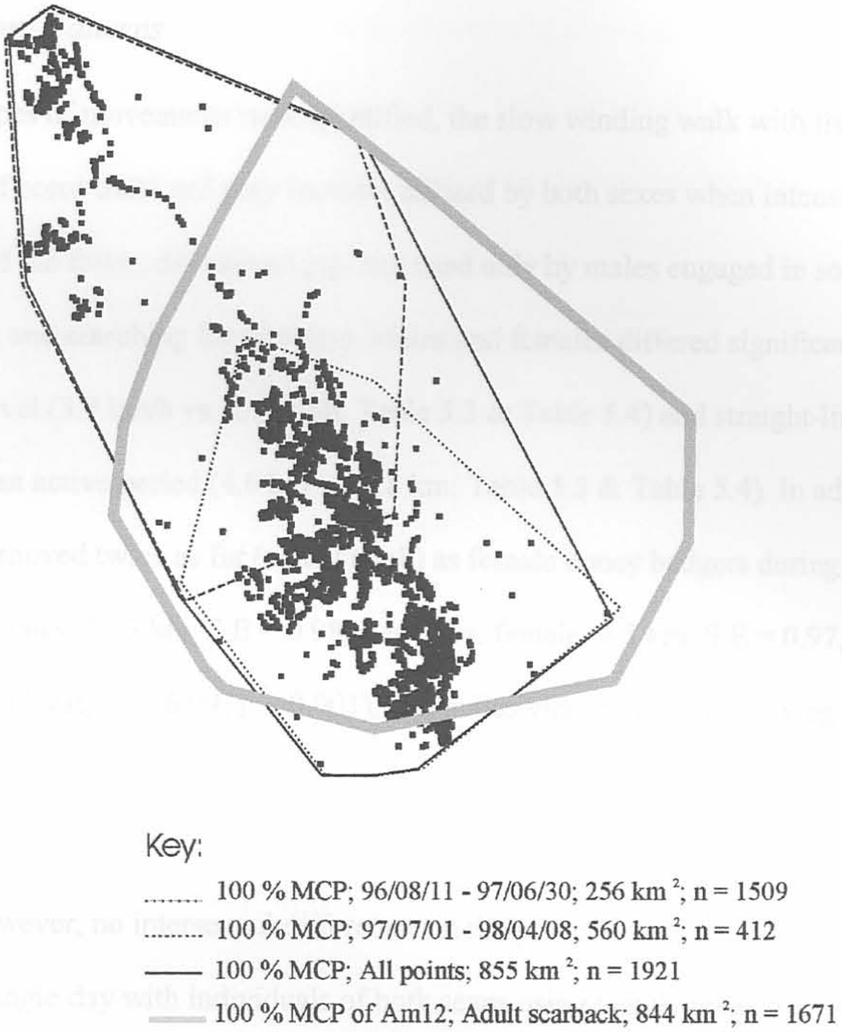


Figure 5.8 Increase in the size of a young male's home range over a 20 month period (100 % MCP of all points; Am 4), showing the initial relatively small home range for 11 months followed by a rapid expansion and shift in home range area. The home range of an adult scarback male (Am12; dominant male in the area; Chapter 7) is also shown for comparison.

5.4.2 Movement Patterns

Overall two types of movements were identified, the slow winding walk with frequent investigation of scent trails and prey burrows utilized by both sexes when intensively foraging (Chapter 2) and the faster, directional jog- trot used only by males engaged in social activities (scent marking and searching for females). Males and females differed significantly in both their rate of travel (3.7 km/h vs. 2.1 km/h; Table 5.3 & Table 5.4) and straight-line distances moved during an active period (4.6 km vs. 1.8 km; Table 5.3 & Table 5.4). In addition, male honey badgers moved twice as far (actual track) as female honey badgers during a single active period (males: 13.7 km, S.E = 0.98, n = 84 vs. female: 7.5 km, S.E = 0.97, n = 41; Mann-Whitney U test, Z = -6.99; $p < 0.001$), and males were capable of moving 40 km actual distance in 4.3 h.

There were, however, no intersexual differences in the percentage of their home range area traversed in a single day with individuals of both sexes using a daily area covering an average of 3 % of their total home range (100 % MCP). There appeared to be no site attachment or philopatry as neither males nor females appeared to concentrate their movements within a specific area of the home range (Figure 5.9; Figure 5.10), except when females had young cubs (Figure 5.11).

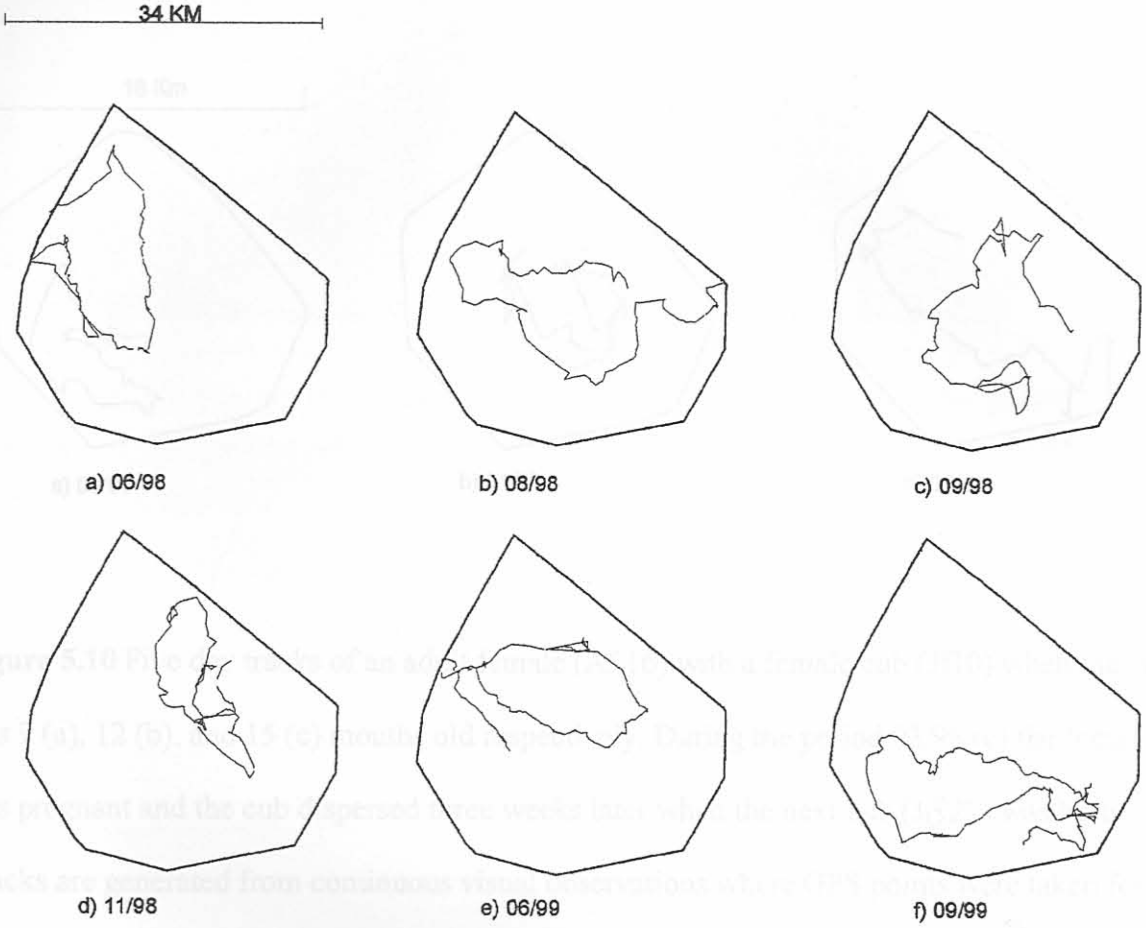
This was also supported by data on burrow use. While both adult males and adult females (with foraging cubs and without cubs) had no fixed den and typically slept in a different burrow each resting period, this was not true of females with cubs less than 3 months of age. Cubs younger than 2-3 months old did not accompany the female foraging (n = 5) and during this period the female foraged in close proximity to the den site moving a maximum of 3.8 km straight line during a foraging period (Figure 5.11). Cub age therefore had a significant effect

Table 5.3 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.

Category	Rate of travel (km / h)	Straight line distance (km) per active period	Percentage of 100 % MCP used / day
Young males	3.0 (27)	3.0 (8)	2.2 (18)
Adult males	3.9 (82)	4.9 (59)	3.3 (38)
Males overall	3.7 (112)	4.6 (67)	2.8 (56)
Adult females	2.4 (41)	1.2 (31)	3.0 (19)
Adult females + den cub	1.7 (45)	0.8 (43)	0.8 (11)
Adult females + forage cub	2.7 (56)	2.6 (49)	3.1 (25)

Table 5.4 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.

Category	Rate of travel (km / h)			Straight line distance (km / active period			Percentage of home range utilized / day		
	U	Z	Sign. level	U	Z	Sign. level	U	Z	Sign. level
Overall ♀ vs. Overall ♂	6063	-3.3	$p < 0.01$	1308	-8.9	$p < 0.001$	1495	-0.3	Not sign
Adult ♂ vs. Adult ♀	1321	-1.9	Not sign	235	5.8	$p < 0.001$	327	-0.6	Not sign
Young ♂ vs. Adult ♂	1094	- 0.1	Not sign	125	-2.2	$p < 0.05$	167	3.1	$p<0.05$
Adult ♀+ den cub vs. Adult ♀ + for. cub	710	3.8	$p < 0.001$	199	-6.7	$p < 0.001$	43	-3.2	$p<0.05$
Adult ♀ vs. Adult ♀+ foraging cub	1118	0.2	Not sign	626	1.3	Not sign	219	0.4	Not sign



a) 06/98 b) 08/98 c) 09/98

d) 11/98 e) 06/99 f) 09/99

Figure 5.9 Five day tracks of an adult male scar-back honey badger (Am12) during different months of the year, over a 15 month period.

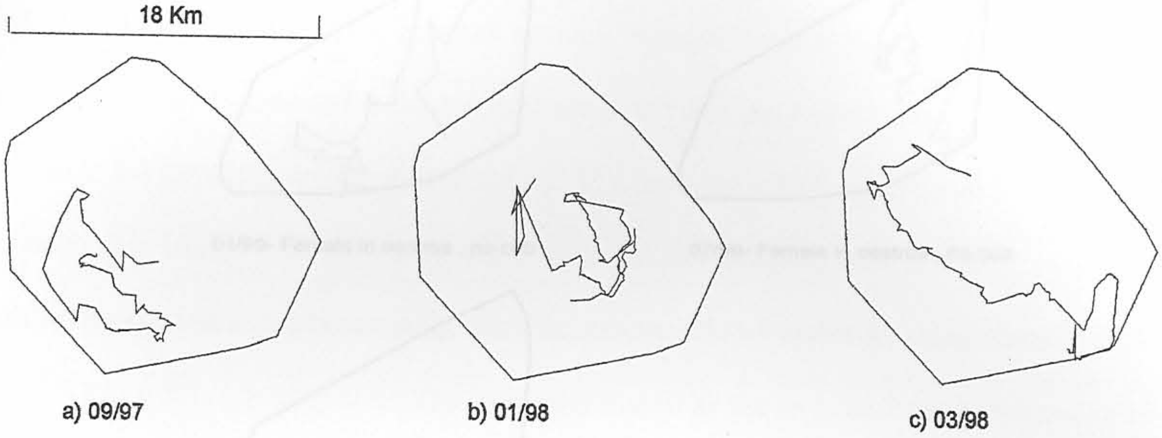
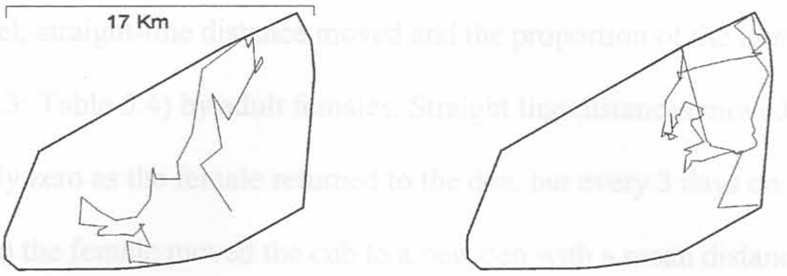
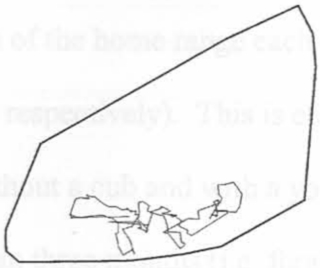


Figure 5.10 Five day tracks of an adult female (Af 16) with a female cub (Jf10) when the cub was 9 (a), 12 (b), and 15 (c) months old respectively. During the period 03/98 (c) the female was pregnant and the cub dispersed three weeks later when the next cub (J♂27) was born. Tracks are generated from continuous visual observations where GPS points were taken for each change in behaviour or at 10-minute intervals.

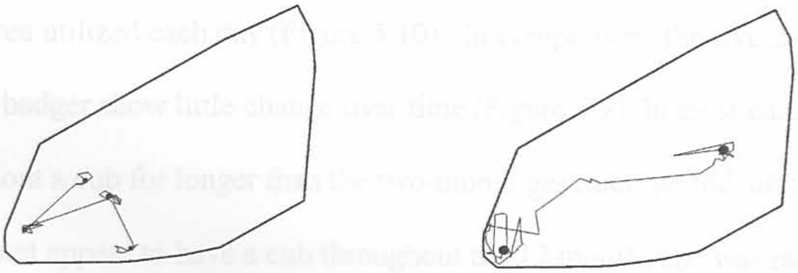


01/99- Female in oestrus , no cub

07/99- Female in oestrus , no cub

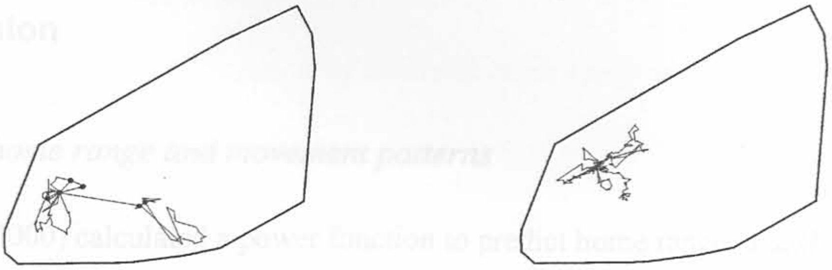


09/99- Female pregnant, no cub



03/99- Female with one month old cub

10/99- Female with one month old cub



05/99- Female with two month old cub

06 /99- Female with three month old cub

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.

on the rate of travel, straight-line distance moved and the proportion of the home range used each day (Table 5.3; Table 5.4) by adult females. Straight line distances moved each active period were usually zero as the female returned to the den, but every 3 days on average (n = 27; range 1-8 days) the female moved the cub to a new den with a mean distance of 2.1 km between dens (range 0.29 – 4.4 km). As a result females with den cubs utilized a significantly smaller proportion of the home range each day compared to females foraging alone (Table 5.4; 0.8 % vs. 3 % respectively). This is clearly shown by the five-day continuous tracks of a female (Af 38) without a cub and with a young cub of varying age (Figure 5.11). Females with cubs older than three months (i.e. foraging cubs) did not differ significantly from adult females without cubs in their rate of travel, straight-line distance moved or the percentage of the home range area utilized each day (Figure 5.10). In comparison, the five day-tracks of an adult male honey badger show little change over time (Figure 5.9). In most cases females were seldom without a cub for longer than the two-month gestation period, although one adult female (Af7) did not appear to have a cub throughout the 17 months she was radio-marked (Table 5.1).

5.5. Discussion

5.5.1 Female home range and movement patterns

Johnson *et al.* (2000) calculated a power function to predict home range area (HR) in mustelids in general, $HR = 1.74M^{0.88}$ and non- social mustelids in particular, $HR = 2.26M^{1.31}$ where M is the average mass of adult females. This predicts a home range size for a female honey badger of about 8.7 km^2 and 24.7 km^2 respectively, 5 - 16 times smaller than the observed home range of female honey badgers in the KTP.

For an adult female, home range size should be large enough to include sufficient food to meet its energetic requirements (Goodrich & Buskirk, 1998), but female honey badgers are seldom alone as they are usually accompanied by a single dependent cub. The cub has an unusually long period of dependency in the KTP (12 –14 months; Chapter 7), during which time it is entirely provisioned by the female (Chapter 2), and the female therefore has to meet not only her own but also the cub's energetic requirements. A female and a dependent male cub (8 –8 kg) that is eight months of age or older will have a combined group mass of at least 15 kg (Chapter 2, section 2.4.4.1). A predicted home range based on this group mass is 78.5 km ^{2} (using $HR = 2.26M^{1.31}$; Johnson *et al.*, 2000), which is more similar to the observed female home range size in the KTP.

A comparison of similar sized mustelids (female mass > 5 kg; Figure 5.12) shows that the home range size for female honey badger in the KTP is smaller than home range of the wolverine *Gulo gulo* (10.6 kg; 405 km^2; Hornocker & Hash, 1981; Johnson *et al.*, 2000), but is substantially larger than the home ranges reported for all other similarly sized mustelids. In the honey badger, female home range size is well beyond the upper confidence limits described by the regression of female body mass and home range area for all mustelids in general, and non social mustelids in particular (Johnson *et al.*, 2000). The honey badger is directly comparable to the American badger in size ($\bar{x}$ female mass = 6.3 kg) and foraging habits as both catch the majority of prey through digging with a largely carnivorous diet that does not differ by sex (Chapter 2; Minta, 1993). Yet, the average home range of the American badger is 3 - 4 km^2 (Minta, 1993; Goodrich & Buskirk, 1998), 35 times smaller than the average home range of the female honey badger.

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) with the following scientific names: American badger *Taxidea taxus,* European river otter *Lutra lutra*; North American river otter *Lontra canadensis*; Indian smooth coated otter *Lutrogale perspicillata*; European badger *Meles meles*; sea otter *Enhydra lutris* and giant otter *Pteronura brasiliensis.*

Home range size has been found to be inversely proportional to available prey biomass (Harestad & Bunell, 1979; Hixon, 1980; Mares & Lacher, 1987; Sandell, 1989), and the extensive home ranges of the wolverine have been related to a scavenging lifestyle that dictates seasonally long movements over a relatively large area in search of carrion (Hornocker & Hash, 1981). The limiting resource for female honey badgers in the southern Kalahari is also likely to be food (Powell, 1979; Gittleman & Harvey, 1982; Erlinge & Sandell, 1986). It is therefore likely that the large home ranges of female honey badgers in the KTP are largely a consequence of low prey availability in this semi-arid environment. However, the large home ranges may also be at least partly a function of the "group mass" of a female and her dependent cub, as cubs are provisioned for an unusually long period. Overall home range size may therefore reflect the area required to support a female and a large dependent cub.

Since data on diet and foraging behaviour (Chapter 2) have shown that the dry season is the lean season for the honey badger in the KTP, it was expected that female honey badgers would show a significant seasonal change in home range size and home range overlap to account for decreasing prey availability in the dry season (Chapter 2), but this was not the case. There was no indication that females increased home range area in the dry season, and while the percentage overlap in neighbouring female home ranges tended to decrease, this was not significant. Lindstedt *et al.* (1986) suggested that an animal's metabolic requirements are not only defined over chronological time but also over biological time, and an animal may therefore define its home ranges according to critical biological periods, such as breeding (Johnson *et al.*, 2000). Cub age has a significant effect on home range area and movement patterns of female honey badgers, and since breeding is asynchronous in the KTP (Chapter 7) this may obscure seasonal changes in home range size.

Ranges of adult female honey badgers were particularly small for the first three months after parturition as their movements were constrained by having a young cub in a den. This effect of cub age on home range size has been documented in a variety of mustelid species (Melquist & Hornocker, 1983; Reid *et al.*, 1994; Kruuk, 1995) and is particularly pronounced in the larger species with altricial young i.e. otters (Kruuk, 1995), and in this case the honey badger.

While there was a large amount of overlap between neighbouring females (25 %), space use appeared to be stable with home range centres regularly spaced within an exclusive core area of an average 26 km^2. The female spacing pattern therefore resembles a loose form of territoriality, although in contrast to other solitary mustelids, they do not defend a fixed space (Powell, 1979; Johnson *et al.*, 2000). The lack of defence may simple be due to the large home ranges being economically indefensible (Brown, 1964; Brown & Orians, 1970). The large amount of overlap suggests spatial and temporal variation in food resources (Brown & Orians, 1970; Erlinge & Sandell, 1986; Sandell, 1989) but may also be influenced by asynchronous breeding as neighbouring females with different aged cubs will require differing amounts of area to fulfil their energetic needs. This allows for a large amount of overlap since females can avoid each other temporally and gain solitary access to shared resources. On no occasion were two females observed to interact despite the large overlap in home ranges (Chapter 7). In other carnivores scent marks have been shown to provide temporal information of space use of other individuals, and animals avoided using areas that had been recently marked by conspecifics (Clapperton, 1989; Gorman & Trowbridge, 1989). In female honey badgers token urination in holes along the foraging path was common and these scent marks may mediate spatio–temporal separation (Chapter 6).

5.5.2 Male home ranges and movement patterns

As predicted male honey badgers have significantly larger home ranges than females, however the intersexual differences in home range size exceeds the values predicted from size dimorphism alone. This suggests that factors other than energetics affect male home range size (Sandell, 1989). During a preliminary study of the honey badger in Mana Pools National Park, Zimbabwe, a home range of 95 km ^{2} (n = 36 points; 100 % MCP) was measured for an adult male honey badger (Begg, 1995). This is the only other published record of a home range for the honey badger, and while it is substantially smaller than the adult male home range recorded in the KTP, it is a minimum value and still larger than predicted.

In solitary carnivores, it is generally agreed that while female spacing patterns are determined by the abundance and dispersion of food, male spatial organisation at least during the mating season is largely determined by the distribution of females (Lindstedt *et al.*, 1986; Sandell, 1989; Johnson *et al.*, 2000). Erlinge & Sandell (1986) provided evidence for this in the stoat *Mustela erminea,* where the movement patterns of males was observed to changes markedly in the mating season, and this change was attributed to a switch in the critical resources from food to mates.

Unlike most mustelids, the honey badger does not have a distinct breeding season in the KTP (Chapter 7) with the result that receptive females are the limiting resource for males throughout the year. The lack of seasonal differences in the home range size of adult males is therefore expected. In terms of resource characteristics, adult female honey badgers in oestrus are unpredictable and scarce resources in space (large home ranges, moving targets) and time (no breeding season), with a long time to renewal (long birth interval) and a high degree of competition between males for the resource (Chapter 7).

Imms (1987) argued that the temporal distribution of sexually receptive females is the main factor determining male spacing patterns and that if individual females become receptive irregularly through time (i.e. asynchronous reproduction), as occurs in the honey badger, then males should adopt a transient use of space resulting in overlapping home ranges. Minta (1993) added that in the American badger *Taxidea taxus* (which shows a similar pattern of male home ranges overlapping with other males and several females but on a smaller scale), a male that sequesters a single female that is not ready to breed will lose opportunities for monitoring and breeding with other females. Males, therefore, attempt to maximize breeding frequency by not only overlapping the smaller female home ranges, but also by moving faster than females (Sandell, 1986). Both of these predictions are supported in this study where males encompass the home ranges of at least 13 female honey badgers and move faster and further than females and yearling males within a non-territorial system. These findings are therefore consistent with the hypothesis that the density and unpredictability of receptive females is driving male spatial organisation. As a result males employ a roaming tactic rather than a staying tactic (Sandell & Liberg, 1992).

Young males are distinct from older males in that they have smaller home ranges, and they move slower and shorter distances on a daily basis. The average home range size of young males is consistent with the predicted value based on metabolic needs alone. This suggests that the limiting resource for young males is food, not receptive females, and they therefore appear to be more similar to females than adult males. This is supported by data on scent marking behaviour where young males were observed to use token urination in common with female honey badgers, but this form of scent marking was not observed in adult males.
It is probable that the increase in young male home range size at a certain age is associated with sexual maturity (i.e. females become the limiting resource rather than food), and it is

therefore associated with a switch to latrine scent marking behaviour (Chapter 6), an increase in testes size and the development of a back scar from male-male competition (Chapter 7).

In both sexes neighbouring home ranges overlap more than 10 % and in adult males in particular home ranges overlap extensively. In males the typical mustelid pattern of intrasexual territoriality (Powell, 1979) is therefore not supported, and there is no evidence from visual observations that adult males actively defend a fixed space. In contrast, adult females avoid each other temporally and female home ranges are regularly spaced with an exclusive core area. Although females also do not appear to actively defend a fixed space (Maher & Lott, 1995), the female spacing pattern does appear to be a loose form of territoriality.

In common with other mustelids, the spatial organisation suggests a polygynous or promiscuous mating system e.g. river otter *Lontra canadensis* (Melquist & Hornocker, 1983; Reid *et al.*, 1994), wolverine *Gulo gulo* (Lande, 1997); American badger *Taxidea taxus* (Minta, 1993); stoats *Mustela erminea* (Erlinge & Sandell, 1986).

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