Spatial organization of the honey badger *Mellivora capensis* in the southern Kalahari: home-range size and movement patterns

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Abstract

Radio-tracking locations of 25 individuals (13 females; 12 males) and visual observations of nine habituated individuals were used to investigate the spatial organization and movement patterns of the honey badger *Mellivora capensis* in the southern Kalahari. The home ranges of adult male honey badgers ($541 \pm 93 \, \text{km}^2$) were significantly larger than the home ranges of adult females ($126 \pm 13 \, \text{km}^2$). Female home-range size was five times larger than predicted from body mass. The extensive home ranges of females were likely to be a function of relatively low prey availability in the semi-arid Kalahari and the long period of cub dependence (12–16 months). While mean home-range overlap in females was moderate (13%) and home-range centres were regularly spaced, females did not appear to actively defend a territory and no direct interactions between females were observed. Scent marking appears to mediate spatio-temporal separation and females show a loosely territorial spacing pattern. In contrast, males did not support the typical mustelid pattern of intra-sexual territoriality but instead encompassed the overlapping home ranges of up to 13 females. Males and females differed significantly in their rate of travel ($3.8 \pm 0.3 \, \text{km/h}$ *vs* $2.7 \pm 0.2 \, \text{km/h}$), straight line ($6.2 \pm 0.5 \, \text{km}$ *vs* $2.4 \pm 0.2 \, \text{km}$) and actual distance ($13.8 \pm 0.9 \, \text{km}$ *vs* $7.7 \pm 0.7 \, \text{km}$) 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 tended to have smaller home ranges ($151 \pm 45 \, \text{km}^2$) than adult males and showed a spacing pattern more similar to adult females than adult males. In common with other solitary mustelids, the spatial organization suggests a polygynous or promiscuous mating system.

Key words: honey badger, *Mellivora capensis*, ratel, Kalahari, spatial organization, home range

INTRODUCTION

Spatial organization 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). 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, Macdonald & Dickman, 2000).

The honey badger *Mellivora capensis* is a relatively large mustelid (6–14 kg) that has not been well studied

previously 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. This paper forms part of a broader study on the feeding ecology and social organization of the honey badger in the southern Kalahari (Begg *et al*., 2003*a,b*; 2004) and aims to provide a preliminary investigation of the spatial organization of the honey badger and possible factors affecting home-range size and movement patterns.

In carnivores, it has repeatedly been shown that home-range size appears to scale allometrically with body mass with a greater rate than expected from basal metabolic rate or daily metabolic needs (Reiss, 1988). A variety of power functions of body mass has been derived to predict home-range area in carnivores (McNab, 1963; Harestad & Bunnell, 1979; Gittleman & Harvey, 1982; Lindstedt, Miller & Buskirk, 1986; Swihart, Slade & Bergstrom, 1988) and more recently in mustelids in particular (Johnson *et al*., 2000). Honey badgers show

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moderate sexual size dimorphism with males a third larger than females (Begg *et al.*, 2003*a*) and inter-sexual differences in home-range size are therefore expected. However, males and females show few differences in diet and foraging behaviour and no differences that can be directly attributed to sexual size dimorphism (Begg *et al.*, 2003*a*).

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).

As part of this study it has been shown that the honey badger is a solitary forager with a wide, largely carnivorous diet. While small mammals are the staple prey throughout the year, reptiles, scorpions, young of larger mammals and insects are seasonally important. Since the dry season (May to August) is the lean season for the honey badger in the southern Kalahari, with decreased consumption rates and increased foraging time (Begg *et al.*, 2003*a*), it is predicted that female honey badgers will show seasonal changes in home-range use and movement patterns. 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 (Begg *et al.*, 2004).

METHODS

Study area

The study was initiated in July 1996 and continued until December 1999 (42 months) in the semi-arid Kgalagadi Transfrontier Park (KTP), South Africa. Details of the study area have been provided previously (Begg *et al.*, 2003*a*). For the purposes of this paper 2 seasons are distinguished, the wet season from September to April when the mean monthly temperature is approximately 20 °C or higher and the majority of rain falls, and the dry season from May to August when the mean monthly temperature is below 20 °C and rainfall is rare (Mills & Retief, 1984).

Data collection

Details of capture, radio-marking and habituation techniques have been presented in detail previously (Begg *et al.*, 2003*a,b*) and will only be outlined here. Whilst sedated, 25 individuals (13 females and 12 males) were fitted with Telonics radio collars. All collars were removed from the honey badgers before the end of the battery life or at the end of the study period. A wildlife veterinarian subsequently implanted 10 of the radio-marked adults (5 females and 5 males) and 3 large cubs (1 male, 2 females) with intraperitoneal radio implants. All individuals were weighed and standard measurements taken (Begg *et al.*, 2003*a*).

Adult male honey badgers were broadly divided into 2 age categories based on tooth wear, body size and condition: young adult (estimated age of 1–3 years, independent from mother) and adult (older than 3 years; Begg *et al.*, 2004). We further divided older adult males into those with and without a back scar (scarbacks and non-scarbacks). The back scar is a raised area or callus in the middle of the back thought to be caused by repeated intra-specific biting in the same area over time (Begg, 2001). Since the scar develops over time scarback males are considered older than non-scarbacks. In addition, the presence of a back scar is related to intimidation postures with scarback males always dominant over non-scarbacks (Begg *et al.*, 2003*b*).

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 to December 1998), and this was later increased to once every 2 weeks for the final year of fieldwork (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, day-time, 3-hour flight when honey badgers were likely to be resting in a burrow 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 2-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 detection distance was greatly reduced (< 2 km) when a honey badger was in a burrow. Radio implants were less powerful with a detection distance of < 2 km.

Over 2000 h were spent habituating 9 radio-marked adult badgers (5 females with 5 cubs, 4 adult males) and 2 young males to the vehicle until they could be followed without any obvious influence on their behaviour. Over the course of the study 5461 h were spent with habituated badgers (females: 2881 h; males: 2580 h; Table 1). Selected animals were followed continuously for observation periods ranging from 1 to 12 days (mean = 4 days, $n = 91$ observation periods) with an additional 57 short observation periods (< 24 h) ranging

Table 1. Study population of honey badgers *Mellivora capensis* used for home-range analysis showing the number of months each individual was radio tracked and the number of hours of observation of habituated (H) individuals through the 4-year study period. Bold indicates the data used to calculate annual home ranges for each individual

| Individual | Months followed | | | | | Total hours observed |
	1996	1997	1998	1999	Total	
Adult females						
Af07 (H)	1	**12**	4	0	17	263
Af15	3	3	0	0	6	–
Af16 (H)	0	2	**12**	3	17	771
Af17	**6**	1	0	0	7	–
Af20 (H)	0	0	**12**	**8**	20	189
Af25 (H)	0	0	**7**	**10**	17	172
Af30	0	0	1	**10**	11	–
Af31	0	0	**8**	3	11	–
Af34	0	0	**12**	3	15	–
Af38 (H)	0	0	0	**12**	12	1486
Total	10	18	54	51	133	2881
Young males						
Ym14	0	0	**6**	0	6	–
Ym11	0	0	**6**	**6**	12	–
Ym04 (H)	**6**	2	0	0	8	422
Adult males						
Am05	**6**	0	0	0	6	–
Am09	0	**8**	**7**	0	15	–
Am43 (H)	0	0	0	**7**	7	303
Am04 (H)	0	**9**	1	0	10	304
Am24 (H)	0	0	**8**	0	8	202
Am12 (H)	0	3	**12**	**9**	24	1226
Total	6	20	28	16	70	2035

from 45 min to 20 h. At the start and end of each activity period (resting position to resting position) 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. In addition, prey items were recorded visually and biomass values for prey items were estimated from data in the literature (Begg *et al*., 2003*a*). For individual females, the biomass of individual prey items caught during each active period was summed to provide an estimate of the biomass consumed per km travelled and per minute spent foraging.

Data analysis

In this study 'home range' is used to refer to the area used by an animal (Burt, 1943) and 'territory' is defined as a more or less exclusive area (< 10% overlap; Sandell, 1989) that is defended by an individual (Brown & Orians, 1970). Home-range area and overlap were evaluated using minimum convex polygons (MCP; Mohr, 1947). The use of MCP allows comparison with studies of other mustelids (Harris *et al*., 1990; Balharry, 1993) and is considered a relatively robust, non-parametric interpretation of home-range size where more than 30 independent points are available (Kenward & Hodder, 1996), although it is sensitive to outliers (Swihart & Slade, 1985*a*,*b*; Kenward, 1987; Balharry, 1993). To assess the effect of outliers, both the 100% MCP and 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 & Hodder, 1996). The merits of these techniques have been widely reviewed (e.g. Kenward, 1987; White & Garrott, 1990). All animal location data were analysed and plotted using the computer program 'Ranges V' (Kenward & Hodder, 1996).

Home-range analysis was complicated by different methods of data collection. For non-habituated individuals data consisted of discrete points from intermittent aerial and ground radio-tracking, while for habituated individuals data points from continuous visual observations were also used. Home-range outlines (100% MCPs) from all individuals known to be in the study area between 1998–1999 were plotted to provide a first description of honey badger density within the study area and to investigate the spatial distribution of neighbouring individuals.

For further home-range analysis, annual home ranges were calculated for individuals that were followed for more than 6 months and for whom more than 30 points were collected within a calendar year (9 females, 6 adult males and 3 young males; Table 1). Where sufficient data were collected for a single individual in consecutive years, a mean annual home range was calculated and used in further analysis (2 females, 2 adult males, 1 young male).

It is acknowledged that points from continuous observations of habituated individuals are temporally autocorrelated and this may result in an underestimate of home-range size (Swihart & Slade, 1985*a*,*b*), but using only statistically independent points would have resulted in the loss of valuable behavioural data (Minta, 1993; Rooney, Wolfe & Hayden, 1998). Rather than using a fixed time interval between fixes, we also calculated the 100% MCP of only resting positions for each habituated individual. Since honey badgers do not have a fixed den site but rest in a different place each day, resting positions can be considered biologically independent as serial locations are separated by a major activity shift (Lair, 1987; Minta, 1992; Creel & Creel, 2002). In addition, since a honey badger is capable of moving 10 km/h, it can cross from one end of the home range to the other in a single active period (2–8 h, Begg, 2001) and consecutive burrow sites can therefore be considered spatially and temporally independent for the purposes of this study (Rooney *et al*., 1998).

Nearest neighbour analysis of range-centre spacing, the degree of overlap between neighbours and linear distances between simultaneous locations of neighbouring females from aerial tracking points (within 3 h) were used to analyse spacing between adult females. Overlap in both males and females was calculated using individual neighbouring pairs for which data were collected within the same calendar year (Table 1).

Table 2. Comparison of the dry (May–August) and wet season (September–April) home ranges in male and female honey badgers *Mellivora capensis* in the Kgalagadi Transfrontier Park. Home ranges were calculated as the 100% minimum convex polygons (MCP) for individuals where at least 30 locations were available for each season in a single calendar year. The home ranges of individual females with cubs in the den (< 3 months old) during the period of analysis are marked in bold. [1] This female was never observed to have a cub

	Home-range size 100% MCP (No. of locations)	
Id. No. & sex	Dry season	Wet season
Females		
Af38–1999	**76 (667)**	**88 (659)**
Af25–1999	104 (31)	89 (91)
Af16–1998	**83 (51)**	184 (552)
Af07[1]–1997	123 (88)	139 (306)
Mean ± SE	*97 ± 11*	*125 ± 23*
Males		
Am12–1998	555 (618)	615 (401)
Am24–1998	699 (188)	426 (73)
Am09–1997	214 (318)	335 (881)
Am04–1997	425 (313)	624 (320)
Mean ± SE	*473 ± 103*	*500 ± 71*

Non-parametric Mann–Whitney U and Kruskal–Wallis tests (Statistica: Stasoft Inc., 1995) were used to investigate sexual and seasonal differences in home-range size and movement patterns. For all home-range analyses the individual honey badger was used as the sampling unit. Spearman's rank correlation was used to assess the associations between prey biomass intake and home-range size. Seasonal differences in the mean percentage of home-range overlap were arcsine transformed to achieve normality and means were compared with the 2-sample, 2-sided Student's t-tests. All statistical tests follow Zar (1999).

RESULTS

Home range

Sufficient data for home-range analysis (> 30 points, followed for more than 6 months in a calendar year) were obtained from 18 radio-marked honey badgers when all points were used (nine adult females; three young males, six adult males; Appendix 1) and 10 individuals when only resting positions were used (five females; one young male and four adult males; Table 2). The mean home-range areas calculated from 100% and 95% MCPs of all points and 100% MCP of only resting positions did not differ significantly in either adult males or females (Kruskal–Wallis test: males, $H_2 = 1.59$, $n = 16$, NS; females, $H_2 = 2.3$, $n = 23$, NS). The results are presented for all methods for comparison with other studies (Appendix 1); however, for further analysis only the mean 100% MCPs of all points were used. No data were collected on home

ranges of young females, as all the females captured were adults. Neither adult males nor adult females showed a significant correlation between the size of the home range (100% MCP & burrow positions) and the number of points collected (Spearman Rank Correlation: Male 100% MCP: $n = 8$, $r_s = 0.48$, NS; Male burrow: $n = 5$, $r_s = 0.52$, NS; Female 100% MCP: $n = 10$, $r_s = 0.23$, NS; Female burrow: $n = 7$, $r_s = 0.46$, NS). In females individual variation in home-range size was relatively large ranging from 85 to 194 km^2 (100% MCP), but habituated females showed no significant individual differences in the average food biomass (in grams) caught per km travelled in either the wet or dry season (Kruskal–Wallis test: wet season, $H_4 = 5.3$, $n = 59$, NS; dry season, $H_4 = 5.2$, $n = 59$, NS) or in the average food biomass caught per minute foraging in either the wet or dry season (Kruskal–Wallis test: wet season, $H_4 = 7.3$, $n = 149$, NS; dry season, $H_4 = 7.3$, $n = 43$, NS). Neither was there a significant correlation between the average amount of food biomass caught per km travelled and home-range area (Spearman Rank Correlation: $n = 6$, $r_s = 0.56$, NS). The habitat of the KTP is remarkably uniform and it is therefore considered unlikely that the large individual differences in female home-range measured reflect differences in prey availability or habitat productivity in different areas. Rather these differences are more likely to be an effect of unequal sampling of females with different aged cubs (see Table 2).

As predicted the overall home ranges (100% MCP) of adult male honey badgers are significantly larger than those of adult females, (females: 126 ± 13 km^2 *vs* males: 541 ± 93 km^2; Mann–Whitney U test: $U = 54$, $n_{female} = 9$, $n_{male} = 6$, $P < 0.001$). In addition, the results suggest that young males ranged over smaller areas than adult males during the period of study (151 ± 45 km^2), although data sets for individual young males were small and the home range variation between individuals was large (82–236 km^2).

To test the prediction that the difference 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 were assumed to be set by metabolic demands (HR_{female}) and male home ranges were predicted as $HR_{female} \times M_{male}/M_{female}$, where M is average mass (Lindstedt *et al.*, 1986). The measured home-range size of adult males was 2.8 times greater than predicted (191 km^2; mean adult female mass $= 6.2 \pm 0.14$ kg; mean adult male mass $= 9.4 \pm 0.23$ kg; Begg *et al.*, 2003a), but the home-range size of young males was similar to the prediction (170 km^2; mean young male mass at independence $= 8.4 \pm 0.1$ kg). This suggests that difference in home-range size between young males and females can be predicted by body mass and metabolic demands, but the difference in home-range size between adult males and adult females was larger than expected from sexual size dimorphism alone.

The annual home ranges of adult males overlapped extensively (74 ± 11%; $n = 8$ overlapping home-range pairs), with almost complete overlap in males for which larger amounts of data were collected (1998 Am 24 &
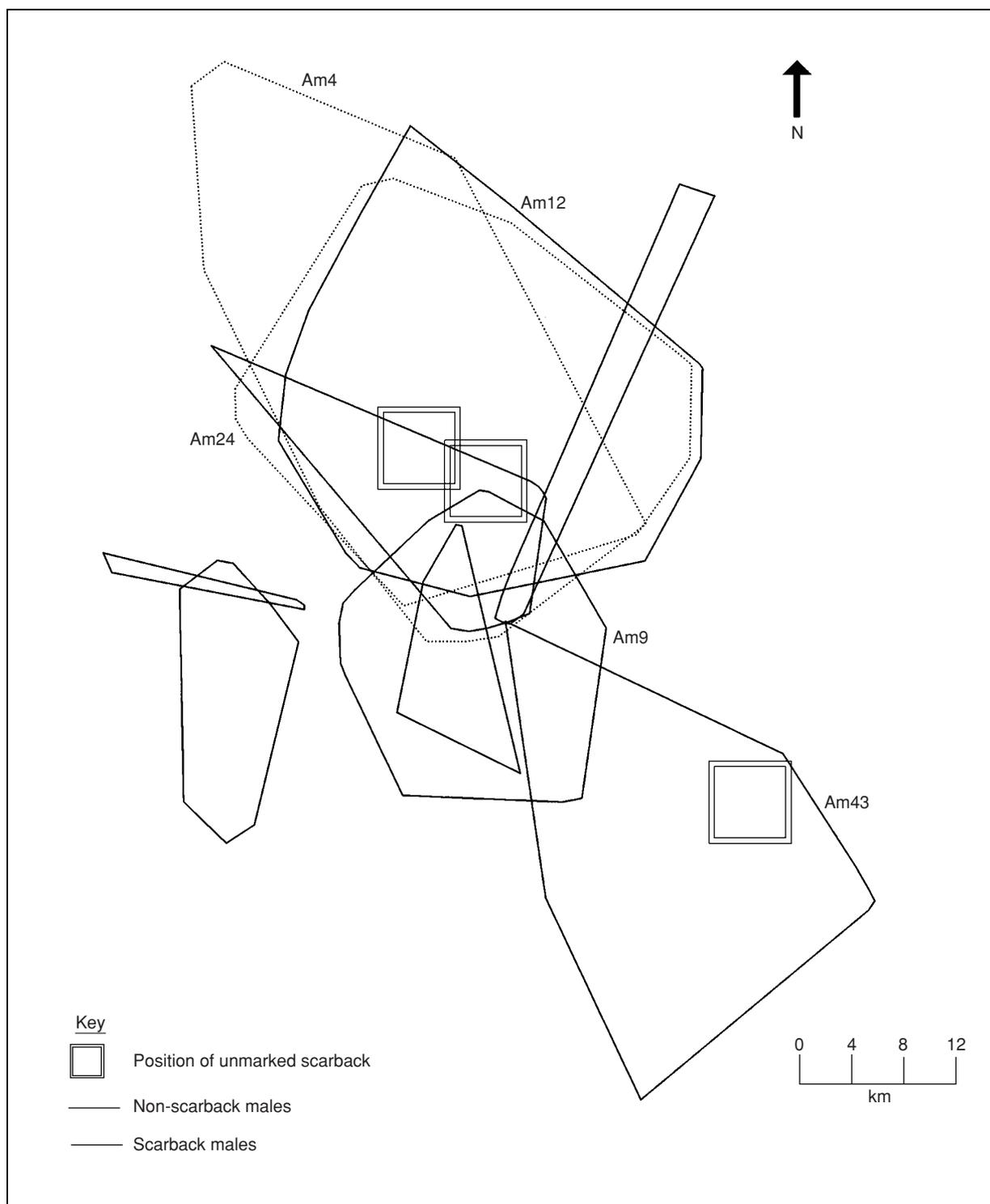
Fig. 1. Home-range outlines (100% minimum convex polygons of all points) of eight radio-marked scarback male honey badgers *Mellivora capensis* and two non-scarback males known to be in the study area between 1998 and 1999. Spot positions of three unmarked scarback males are also shown to provide an indication of the density of male honey badgers.

Am12 = 90%; 1997 Am12 & Am4 = 75%; Fig. 1). Young male home ranges were contained within the home ranges of adult males. There was no evidence that either adult or young males were territorial, however males were observed to compete directly for access to receptive females by ritualized, agonistic encounters and occasional aggressive interactions (Begg, 2001) mediated

by a dominance hierarchy and scent-matching (Begg *et al.*, 2003*b*).

Indepth data from a scarback, dominant male showed that at least 13 females were encompassed within his home range (Am12; Fig. 2). He was seen to interact with nine of these females and five other adult males with overlapping home ranges. Eight known males (four adult scarback

Table 3. A comparison of the mean rate of travel, and actual and straight line distances moved per active period in adult male and female honey badgers *Mellivora capensis* with and without cubs. [1] Sample size refers to the total number of active periods (resting to resting) individuals within each category were continuously observed, i.e. data for individuals within each category were pooled (see Methods)

Category	Rate of travel (km/h) Mean ± SE (n)[1]	Straight line (km/active period) Mean ± SE (n)[1]	Actual distance (km/active period) Mean ± SE (n)[1]
Adult males (n = 4)	3.8 ± 0.3 (112)	6.2 ± 0.5 (48)	13.8 ± 0.9 (81)
Adult females alone (n = 2)	2.6 ± 0.2 (41)	2.1 ± 0.2 (22)	8.0 ± 1.3 (24)
Adult females + forage cub (n = 3)	2.7 ± 0.2 (58)	2.6 ± 0.3 (35)	7.7 ± 0.9 (39)
Adult females (alone + forage cub; n = 5)	2.7 ± 0.2 (99)	2.4 ± 0.2 (57)	7.7 ± 0.7 (63)
Adult females + den cub (n = 2)	1.8 ± 0.2 (45)	0	4.7 ± 0.6 (33)

males, two adult non-scarback males; two young males) were also observed to interact with some of these same females. On a further eight occasions non-radio-marked males were seen within this same area.

The annual home ranges of neighbouring female honey badgers (100% MCP) overlapped less than males, with the amount of overlap ranging from 5.5% to 38% with an average overlap of $13 \pm 2.3\%$ ($n = 10$ overlapping home range pairs). Since this analysis only includes those females for which sufficient data were available for determination of home-range size, the actual level of overlap for all females known to be within the study area is likely to be higher (Fig. 2). Despite this overlap female honey badgers were never seen to interact. The mean distance between simultaneous aerial tracking points (within a 3 h flight) of neighbouring females was 12.5 ± 5.9 km ($n = 80$), and neighbouring females were never recorded closer than 2.6 km. Nearest neighbour analysis of female range centres of all females known to be within the study area during 1998–1999 (Ranges V; Kenward & Hodder, 1996) showed that the range centres were significantly more regularly spaced than expected from a spacing based on 1000 random locations ($n = 9$; $t = 3.3$, $P < 0.05$).

Two radio-marked female cubs dispersed immediately on becoming independent (i.e. away from their mother's for more than 2 days and foraging independently). One female cub (J10) was located 1.1 km from her mother in April 1998 (on the predicted birth of the mother's next cub), within 2 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 5 months after dispersal (September, 1998). In contrast, male cubs appeared to remain within or close to their natal home range for at least several months after independence ($n = 3$, Am14, Am33, Am11). For example one male (Am33) became independent at approximately 16 months old but after 2 months alone he re-joined his mother and remained with her until the end of the study, by which time he was more than 2 years old. Despite at least two periods of mating and courtship she did not appear to have another cub. A young male honey badger that regularly followed for 20 months initially had a relatively small home range (Am4; 256 km²; $n = 1509$ points; August 1996 to April 1997) but was then observed to extend his home range into a new area (560 km²; $n = 412$; May 1997–Apr 1998; Fig. 3). 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 and eat the young cub of a female (infanticide).

There was no evidence for a seasonal difference in home-range size in either males or females (Mann–Whitney U test Females: $U = 12$, $n_1 = n_2 = 4$, NS; Males: $U = 7$, $n_1 = n_2 = 4$, NS; Table 2).

Movement patterns and home-range use

For analysis of movement patterns, each active period (a continuous observation period from resting behaviour to resting behaviour) was used as the sampling unit with data pooled from different individuals. This was considered justified since no significant individual differences in movement patterns were found within the adult males or adult females groups (Kruskal–Wallis test Females: rate of travel $H_4 = 5.72$, $n = 81$, NS; actual distance $H_4 = 0.89$, $n = 44$; NS; straight line distance $H_4 = 3.91$, $n = 42$, NS; Males: rate of travel $H_3 = 3.91$, $n = 112$, NS; actual distance $H_3 = 6.31$, $n = 81$, NS; straight line distance $H_3 = 4.12$, $n = 48$, NS).

Neither males nor females concentrated their movements within a specific area of the home range (Fig. 4), except when females had cubs younger than 3 months of age (Fig. 4c). In adult males and adult females with cubs older than 3 months of age individuals typically slept in a different burrow each resting period. However, cubs younger than 2–3 months old ('den cubs') did not accompany their mothers foraging ($n = 5$ mother–cub pairs) and cubs were left in a den. Females with den cubs typically reused burrows for an average of three consecutive days ($n = 27$; range 1–8 days) before moving the cub to a new den, with a mean distance of 2.1 km between dens (range 0.3–4.4 km).

No significant differences in the rate of travel (Mann–Whitney U test: $U = 1083$, $Z = -0.8$, $n_{\text{forage cub}} = 58$, $n_{\text{alone}} = 41$, NS; Table 3) straight line distance (Mann–Whitney U test: $U = 327$, $Z = 0.9$, $n_{\text{forage cub}} = 35$, $n_{\text{alone}} = 22$, NS; Table 3) or actual distance (Mann–Whitney U test: $U = 460$, $Z = -0.11$, $n_{\text{forage cub}} = 39$, $n_{\text{alone}} = 24$, NS; Table 3) travelled during an active period were recorded between females without cubs
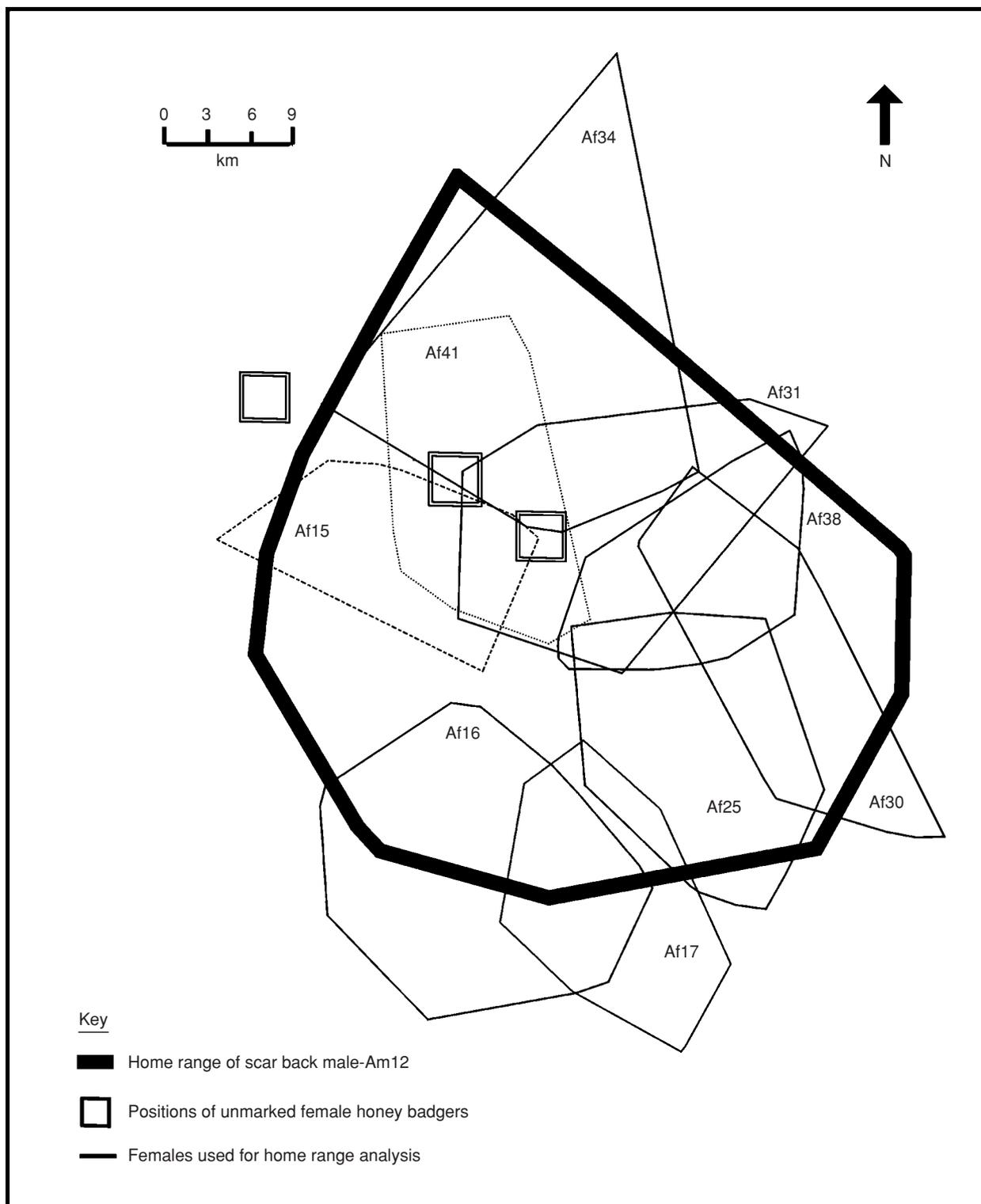
Fig. 2. Home-range outlines (100% minimum convex polygons of all points) of 10 radio-marked female honey badgers *Mellivora capensis* known within the study area between 1998 and 1999, showing the range overlap and size of female home ranges in relation to an adult scarback male honey badger (Am12) using 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.

and females with foraging cubs. However, females foraging alone but returning to cubs in a fixed den site travelled significantly less distance (Mann–Whitney U test: $U = 722$, $Z = 2.45$, $n_{\text{den cubs}} = 33$, $n_{\text{no den}} = 63$, $P < 0.05$) and slower (Mann–Whitney U test: $U = 1218$, $Z = 4.35$, $n_{\text{den cubs}} = 45$, $n_{\text{no den}} = 99$, $P < 0.01$) than
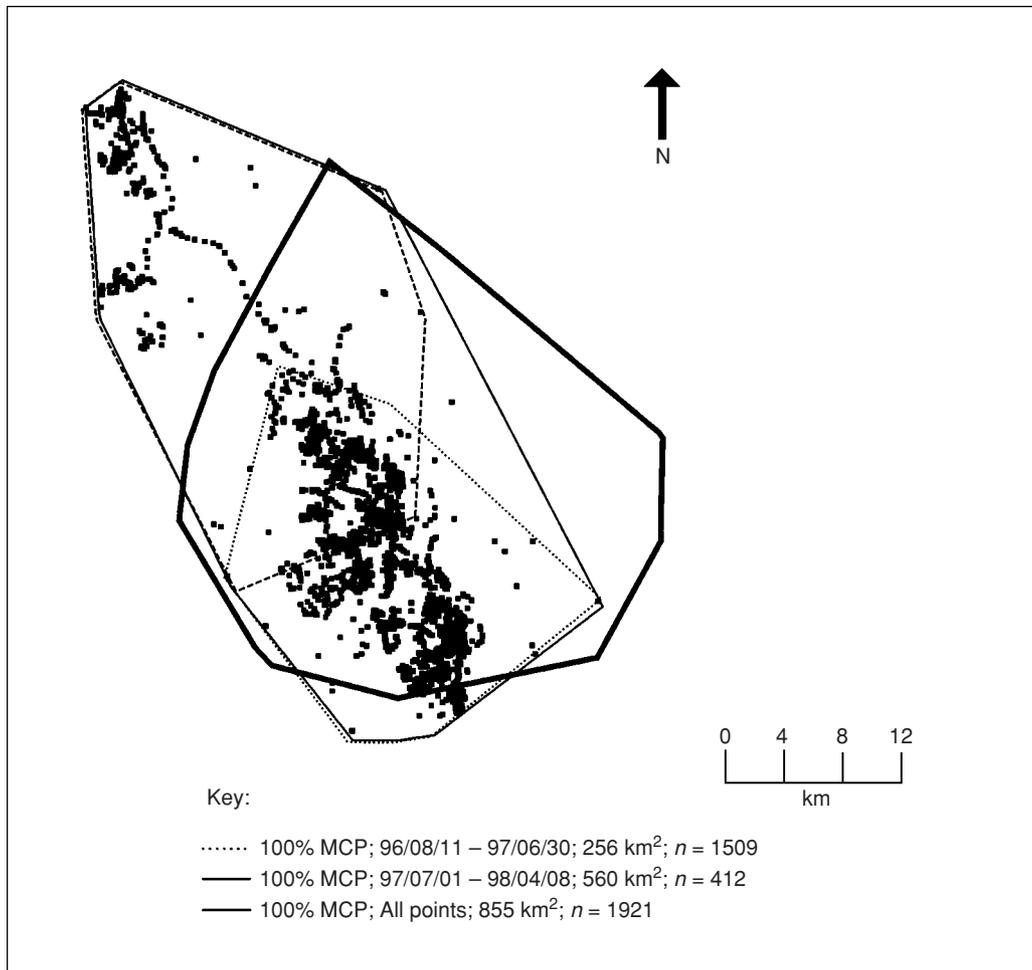
Fig. 3. Increase in the size of the home range of a young male honey badger *Mellivora capensis* over a 20-month period (100% minimum convex polygons of all points; Am 4), showing the initial relatively small home range for 11 months followed by a rapid expansion and shift in home-range area. The home range of an adult scarback male (Am12; the dominant male in the area) is also shown for comparison.

females without a fixed den (Table 3). In addition, females with den cubs used a significantly smaller proportion of the home range each day compared to females with no fixed den (0.8% *vs* 3% respectively; Mann–Whitney U test: $U = 43$, $Z = -3.2$, $P < 0.05$, $n_{\text{den cub}} = 11$; $n_{\text{no den}} = 25$).

Adult males and adult females (without den cubs) also differed significantly in their rate of travel (Table 3; Mann–Whitney U test: $U = 4428$, $Z = -2.52$, $P < 0.05$, $n_{\text{male}} = 112$, $n_{\text{female}} = 99$), straight-line distances moved during an active period (Table 3; Mann–Whitney U test: $U = 399$, $Z = -6.23$, $P < 0.05$, $n_{\text{male}} = 48$, $n_{\text{female}} = 57$), and actual distance travelled (Table 3; Mann–Whitney U test: $U = 1376$, $Z = -4.73$, $P < 0.05$, $n_{\text{male}} = 81$, $n_{\text{female}} = 63$), with adult males typically travelling faster and further between resting sites than females. Males are capable of moving 40 km actual distance in 4.3 h. There was, however, no inter sexual difference in the percentage of home-range area (100% MCP) traversed in a single day with individuals of both sexes using an average of 3% of their total annual home range (females: mean = 3.1%; $n = 44$ observation periods; males:: mean = 3.3%; $n = 38$).

DISCUSSION

Female home range and movement patterns

Johnson *et al.* (2000) calculated a power function to predict home range area (HR) in mustelids in general, $\text{HR} = 1.74\text{M}^{0.88}$ and non-social mustelids in particular, $\text{HR} = 2.26\text{M}^{1.31}$ 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, 5–14 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 energetic requirements (Goodrich & Buskirk, 1998). However, female honey badgers are seldom alone as a single dependent cub usually accompanies them. The cub has an unusually long period of dependency (12–16 months; Begg *et al.*, 2004) and even after weaning at 2–3 months the cub is entirely provisioned by the female. The female therefore has to meet not only her own but also the cub's energetic requirements. A female (mean = 6.3 kg) and a dependent male cub (8–9 kg) that is 8 months
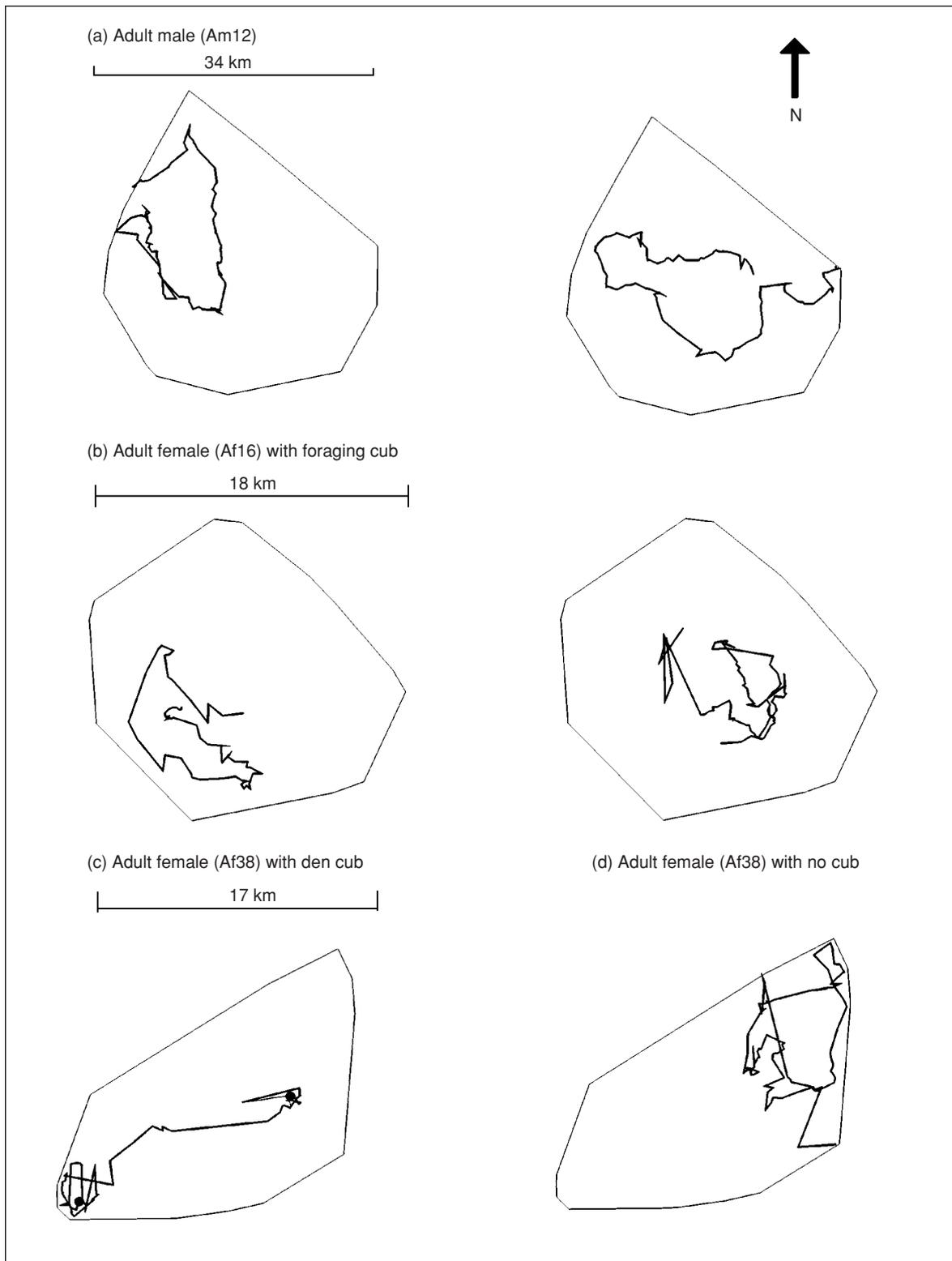
Fig. 4. Five-day tracks of an adult male scarback honey badger *Mellivora capensis* (Am12), and two adult females within their respective 100% minimum convex polygon home-range boundaries. Tracks are generated from continuous visual observations where GPS points were taken for each change in behaviour or at 10-minute intervals, where black dots represent den sites in Af38.

of age or older will have a combined group mass of at least 15 kg (Begg *et al*., 2003*a*). A predicted home-range based on this group mass is 78.5 km^2 (using HR$= 2.26$M$^{1.31}$; Johnson *et al*., 2000), which is more

similar to the observed female home-range size in the KTP.

In the honey badger, female home-range size is well beyond the upper confidence limits described by the
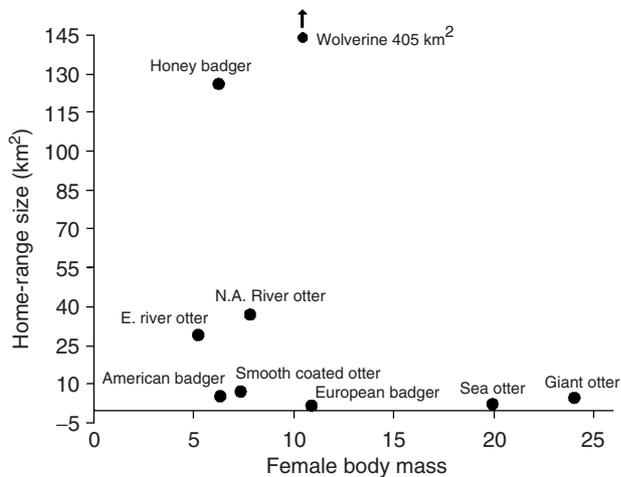
Fig. 5. Comparison of the average home range area in nine mustelids (>5 kg), showing the relatively large home range of the honey badger *Mellivora capensis* and the wolverine *Gulo gulo*. All data except for the honey badger are from Johnson *et al*. (2000) with the following scientific names: American 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*.

regression of female body mass and home-range area for all mustelids in general, and non-social mustelids in particular reported in Johnson *et al*. (2000; Fig. 5). While the honey badger is directly comparable to the American badger in size (mean 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 (Minta, 1993; Begg *et al*., 2003b), the average home range of the American badger is 3–4 km² (Minta, 1993; Goodrich & Buskirk, 1998), 35 times smaller than the average home range of the female honey badger. Important differences between the American badger and the honey badger may be the more specialized diet of the American badgers, which often feeds almost exclusively on any rodent that is abundant, and the shorter period of cub dependence (< 6 months; Long, 1992).

When compared directly with other similarly sized mustelids, the home range of female honey badgers is only smaller than that of the wolverine *Gulo gulo* (10.6 kg; 405 km; Hornocker & Hash, 1981; Johnson *et al*., 2000). 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 semi-arid KTP is also likely to be food and it is also likely that their large home ranges are largely a reflection of low prey availability. Studies in more productive habitats should elucidate this further. However, these large home

ranges may also be partly a function of the 'group mass' of a female and her dependent cub during the unusually long provisioning period. The large home ranges may encompass patches that are infrequently visited when cubs are young allowing for overlap between neighbouring females and temporal avoidance, but such patches might be vital at certain times, such as during the final months of cub dependence (Johnson *et al*., 2000).

Since data on diet and foraging behaviour have shown that the dry season is the lean season for the honey badger in the KTP with decreased consumption rates and increased foraging times (Begg *et al*., 2003a), it was expected that female honey badgers would show a significant seasonal change in home-range size to account for decreasing prey availability in the dry season, but this was not the case. 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 rather define its home ranges according to critical biological periods, such as breeding (Johnson *et al*., 2000). Insufficient fixes were collected to specifically analyse the effects of pregnancy, lactation and cub age on home-range size. However, since there is no specific breeding season for honey badgers in the KTP, it is likely that effects of breeding and cub age on movement patterns and metabolic requirements are masking any seasonal variation in home-range size due to differences in prey abundance. In particular, the restricted movements of females during the first 3 months after parturition, when they are constrained by having a young cub in a den, are likely to effect overall seasonal home-range sizes. 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 such as otters (Kruuk, 1995).

While mean annual home-range overlap in females was moderate and home-range centres were regularly spaced, females did not appear to actively defend a territory and no direct interactions between females were observed. The lack of defence may simply be due to the large home ranges being economically indefensible (Brown, 1964; Brown & Orians, 1970). Females appeared to avoid each other temporally thereby gaining solitary access to resources. In other carnivores scent marks have been shown to provide temporal information on space use of 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 are likely to mediate this spatio–temporal separation (Begg *et al*., 2003b). Females are therefore considered loosely territorial.

Male home ranges and movement patterns

As predicted, male honey badgers have significantly larger home ranges than females, however the intersexual difference in home-range size exceeds the values predicted from size dimorphism alone. 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 a 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 from body size alone.

In solitary carnivores it is generally agreed that male spatial organization, at least during the mating season, is largely determined by the distribution of females (Erlinge & Sandell, 1986; Lindstedt *et al*., 1986; Sandell, 1989; Johnson *et al*., 2000). However, unlike most mustelids, the honey badger does not have a distinct breeding season in the KTP (Begg *et al*., 2004) and receptive females are likely to be a limiting resource for males throughout the year. The lack of seasonal differences in the home-range size of adult males was therefore expected. In terms of resource characteristics, adult female honey badgers in oestrous 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.

Imms (1987) argued that if individual females become receptive irregularly through time (i.e. asynchronous reproduction), 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 who 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 within a non-territorial system. As a result males use a roaming tactic rather than a staying tactic (Sandell & Liberg, 1992). These findings are therefore consistent with the hypothesis that the density and unpredictability of receptive females is driving male spatial organization.

Young males are distinct from older males in that they have smaller home ranges that are consistent with the predicted value based on body size and metabolic needs alone. This suggests that the limiting resource for young males is food not receptive females. This is supported by data on scent-marking behaviour where young males were observed to use token urination in common with female honey badgers. It is probable that the increase in young male home-range size at a certain age associated with a switch to latrine scent-marking behaviour, an increase in testes size and the development of a back scar from male–male competition (Begg *et al*., 2003b) indicates sexual maturity with a switch from food to females as the limiting resource.

In adult males the typical mustelid pattern of intrasexual territoriality (Powell, 1979) was therefore not supported as they did not actively defend a fixed space and showed overlapping home ranges. Instead males adopted a roaming tactic and competed directly for access to receptive females at a mating burrow with interactions mediated by a dominance hierarchy and scent marking (Begg *et al*., 2003b). In contrast, adult females do appear to support a loose form of intrasexual territoriality with spatio-temporal separation maintained by scent marking (Begg *et al*., 2003b). In common with other mustelids, the spatial organization suggests a polygynous or promiscuous mating system for honey badgers in this semi-arid environment.

REFERENCES

Balharry, D. (1993). Social organization in martens: an inflexible system? *Symp. Zool. Soc. Lond*. **65**: 321–345.

Begg, K. S. (1995). Results of the pilot study: breeding ecology and socio-biology of the honey badger *Mellivora capensis*. Unpublished report for the Endangered Wildlife Trust, Johannesburg.

Begg, C. M. (2001). *Feeding ecology and social organization of honey badgers in the southern Kalahari*. Ph.D. thesis. University of Pretoria, South Africa.

Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2003a). Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger *Mellivora capensis*. *J. Zool. (Lond.)* **260**: 301–316.

Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2003b). Scent marking behaviour of the honey badger *Mellivora capensis* (Mustelidae) in the southern Kalahari. *Anim. Behav*. **66**: 917–929.

Begg, C. M., Begg, K. S., du Toit, J. T. & Mills, M. G. L. (2004). Life-history variables of an atypical mustelid, the honey badger *Mellivora capensis*. *J. Zool. (Lond.)* **265**: 19–25.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bull*. **76**: 160–169.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst*. **1**: 239–262.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal*. **24**: 346–352.

Clapperton, B. K. (1989). Scent-marking behaviour of the ferret, *Mustela furo* L. *Anim Behav*. **38**: 436–446.

Clevenger, A. P. (1993). Pine marten (*Martes Martes* L.) home ranges and cativity patterns on the island of Minorca, Spain. *Z. Saugetierkunde* **58**: 137–143.

Creel, S. & Creel, N. M. (2002). *The African wild dog: behaviour, ecology and conservation.* Princeton: Princeton University Press.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197**: 215–223.

Erlinge, S. & Sandell, M. (1986). Seasonal changes in the social organization of male stoats, *Mustela erminea*: an effect of shifts between two decisive resources. *Oikos* **47**: 57–62.

Gittleman, J. L. & Harvey, P. H. (1982). Carnivore home range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* **10**: 57–63.

Goodrich, J. M. & Buskirk, S. W. (1998). Spacing and ecology of North American Badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex. *J. Mammal* **79**: 171–179.

Gorman, M. L. & Trowbridge, B. J. (1989). The role of odour in the social lives of carnivores. In *Carnivore behaviour, ecology and evolution:* 57–88. Gittleman, J. L (Ed.). Ithaca: Cornell University Press.

Harestad, A. S. & Bunnell, F. (1979). Home range and body weight: a re-evaluation. *Ecology* **60**: 389–402.

Harris, S., Cresswell, W. J., Forde, P. G., Trewella, W. J., Woollard, T. & Wray, S. (1990). Home range analysis using radio tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20**: 97–123.

Hixon, M. A. (1980). Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* **115**: 510–530.

Hornocker, M. G. & Hash, H. S. (1981). Ecology of the wolverine in northwestern Montana. *Can. J. Zool.* **59**: 1286–1301.

Imms, R. A. (1987). Male spacing patterns in microtine rodents. *Am. Nat.* **130**: 475–484.

Johnson, D. S. P., Macdonald, D. W. & Dickman, A. J. (2000). An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Rev.* **30**: 171–196.

Kenward, R. E. (1987). *Wildlife radio-tagging: equipment, field techniques and data analysis.* London: Academic Press.

Kenward, R. E. & Hodder, K. H. (1996). *Ranges V: an analysis system for biological location data.* Wareham: Institute of Terrestrial Ecology.

Kruuk, H. (1995). *Wild otters: predation and populations.* New York: Oxford University Press.

Lair, H. (1987). Estimating the location of the focal center in red squirrel home ranges. *Ecology* **68**: 1092–1101.

Lindstedt, S. L., Miller, B. J. & Buskirk, S. W. (1986). Home range, time and body size of mammals. *Ecology* **67**: 413–418.

Long, C. A. (1992). Status and economic importance of the North American badger, *Taxidea taxus* (Schreber). *Small Carn. Conserv.* **7**: 4–7.

Mares, M. A. & Lacher, T. E. (1987). Social spacing in small mammals: patterns of individual variation. *Am. Zool.* **27**: 293–306.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**: 133–140.

Melquist, W. E. & Hornocker, M. G. (1983). Ecology of river otters in west central Idaho. *Wildl. Monogr.* **83**: 1–60.

Mills, M. G. L. & Retief, P. F. (1984). The response of ungulates to rainfall along the riverbeds of the southern Kalahari, 1972–1982. *Koedoe* **1984** (Suppl.): 129–142.

Minta, S. C. (1992). Tests of spatial and temporal interaction among animals. *Ecological Applications* **2**: 178–188.

Minta, S. C. (1993). Sexual differences in spatio-temporal interaction among badgers. *Oecologia* **96**: 402–409.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**: 223–249.

Moors, P. J. (1980). Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos* **34**: 147–158.

Powell, R. A. (1979). Mustelid spacing patterns: variations on a theme by *Mustela. Z. Tierpsychol.* **50**: 153–165.

Reid, D. G., Code, T. E., Reid, A. C. H. & Herrero, S. M. (1994). Spacing movements, and habitat selection of the river otter in boreal Alberta. *Can. J. Zool.* **72**: 1314–1324.

Reiss, M. (1988). Scaling of home range size: body size, metabolic needs and ecology. *Trends. Ecol. Evol.* **3**: 85–86.

Rooney, S. M., Wolfe, A. & Hayden, T. J. (1998). Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Rev.* **28**: 89–98.

Sandell, M. (1986). Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. *Oikos* **47**: 63–70.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behaviour, ecology and evolution*: 164–182. Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.

Sandell, M. & Liberg, O. (1992). Roamers and stayers: a model of male mating tactics and mating systems. *Am. Nat.* **139**: 177–189.

Stasoft, Inc. (1995). *Statistica for Windows: Computer program manual.* Tulsa, Oklahoma.

Swihart, R. K. & Slade, N. A. (1985*a*). Influence of sampling interval on estimates of home range size. *J. Wildl. Manage.* **49**: 1019–1025.

Swihart, R. K. & Slade, N. A. (1985*b*). Testing for independence of observation in animal movements. *Ecology* **6**: 1176–1184.

Swihart, R. K., Slade, N. A. & Bergstrom, B. J. (1988). Relating body size to the rate of home range use in mammals. *Ecology* **69**: 393–399.

Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual selection and the descent of man*: 136–179. Campbell, B. (Ed.). Chicago: Aldine.

White, G. C. & Garrott, R. A. (Eds) (1990). *Analysis of wildlife radio tracking data*. New York: Academic Press.

Zar, J. H. (1999). *Biostatistical analysis.* New Jersey: Prentice-Hall Inc.

Appendix 1. Home-range size of female and male (young and adult) honey badgers *Mellivora capensis* in the Kgalagadi Transfrontier Park, showing the number of points used for each analysis. Home-range area is calculated as the 100% and 95% minimum convex polygon (MCP) of all points within a single calendar year and the 100% MCP from only burrow positions within a single calendar year, where sufficient points are available. Where individuals were followed for 2 consecutive years a mean value was calculated for each individual from annual home ranges. H, habituated. [1] Moved from young male to adult male with associated increase in testes size and development of a back scar during study

Id. No. and age	100% MCP (km^2) Mean (SE)	95% MCP (km^2)	No. Points	Burrow MCP (km^2)	No. Points
Adult females					
Af 20 (H)	$85 + 9$	$74 + 2$	49, 253	$74 + 3$	45, 30
Af 17	96	73	266	–	–
Af 38 (H)	105	99	1326	81	124
Af 34	135	126	38	–	–
Af 30	105	97	154	–	–
Af 25 (H)	105 ± 17	93 ± 17	122, 64	105 ± 17	87, 44
Af 31	147	166	40	–	–
Af 16 (H)	194	145	603	144	78
Af 07 (H)	170	137	394	103	53
Mean ± SE	*126 ± 13*	*108 ± 9*		*101 ± 12*	
Young males					
Ym 14	82	75	87	–	–
Ym 11	137 ± 14	107 ± 13	33, 52	–	–
Ym 04[1] (H)	236	221	931	186	195
Mean ± SE	*151 ± 45*	*134 ± 44*		*186*	
Adult males					
Am 05-scarback	229	130	121	–	–
Am 09-scarback	291 ± 11	256 ± 10	406, 60	213	46
Am 43-scarback (H)	588	346	311	472	44
Am 04 (H)	664	625	778	525	70
Am 24 (H)	776	729	261	575	73
Am 12 scarback (H)	698 ± 8	575 ± 59	1019, 594	565 ± 59	73, 34
Mean ± SE	*541 ± 93*	*443 ± 95*		*485 ± 58*	