- Chapter 7 -

Breeding system and social interactions of the honey badger *Mellivora capensis* in the southern Kalahari.

7.1 Abstract

The mating system of most mustelids has been classified as solitary and polygynous, showing intersexual territoriality with overlapping home ranges between the sexes, although the family also includes five social species. Visual observations of nine habituated honey badgers were used to collect information on intraspecific interactions and life history variables. Breeding was asynchronous with an unusually small litter size of one cub born after a gestation of 50-70 days, with a long time to independence of 12 –16 months. As predicted, the honey badger shows a polygynous mating system. Intraspecific interactions included male-male (male groups, agonistic, aggressive, amicable) and male-female interactions but on no occasion were two adult females seen together. The data suggest that three forms of intrasexual competition influence the relative reproductive success of male honey badgers: direct contests over oestrous females through ritualized agonistic and aggressive interactions, competitive mate searching and sperm competition (large testes). Age (presence of a back scar), mass and testes size all appear to influence the outcome of paired interactions, with a dominance hierarchy maintained through direct interactions and scent- marking. Observations suggest that females are polyandrous i.e. mate with more than one male during a receptive phase and there is some evidence of female choice.

7.2 Introduction

The breeding system of a species is defined as a behavioural strategy for securing mates and it encompasses both sexual selection (the number of mates and the way in which they are obtained) and parental care (Emlen & Oring, 1977). The classical view suggests that the breeding system of a population depends on the ability of one sex (usually males) to acquire mates either by associating with them directly or by defending territories and other resources for breeding, while the limiting sex (usually females) is a commodity to be courted and fought over (Macdonald, 1983; Clutton-Brock, 1989; Sandell, 1989; Sandell & Liberg, 1992). In terms of this classical view, it is suggested that most mustelids are solitary and polygynous and show intra-sexual territoriality with overlapping home ranges between the sexes (Powell, 1979; Moors, 1980; Balharry, 1993). However, this diverse family also includes the group living but solitary foraging European badger *Meles meles* (Kruuk, 1989) and four social otter species (Johnson *et al.*, 2000).

Recent studies have posed serious challenges to this classical view of polygynous systems, both because females have been found to play an active role in mate choice in many taxa and because genetic advances have shown that both sexes often mate with more than one partner (Reynolds, 1996). In addition, there is growing evidence that mating systems vary within species, which supports the view that mating systems result from individual strategies rather than being an evolved feature of each species (Clutton-Brock, 1989; Johnson *et al.*, 2000). For example, the European badger normally forms multi-male, multi female groups in Britain (Neal & Cheeseman, 1996; Kruuk & Parish, 1987), but elsewhere in their range they commonly live solitarily or in pairs with either intra- or inter-sexual territories (Woodroffe & Macdonald, 1993).

The honey badger *Mellivora capensis* is a medium sized (6-14 kg) mustelid with a wide 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 (Harrison & Bates, 1991; Neal & Cheeseman, 1996; F.Cuzin *in litt* 2001). With the exception of a six-week study on its foraging habits in the southern Kalahari (Kruuk & Mills, 1983) there have been no previous field studies of the species, and consequently little is known of its reproductive biology or social organization.

This chapter forms part of a broader study, which has shown that the honey badger is a solitary forager with marked sexual size dimorphism (males a third larger than females; Chapter 2). In addition, investigation of its spatial organisation (Chapter 5) revealed that the honey badger does not show the typical mustelid pattern of intrasexual territoriality (Powell, 1979), instead males had large home ranges that overlapped extensively with other males and encompassed the smaller home ranges of up to 13 females. It is therefore predicted that the honey badger will show a polygynous mating system, however, other sources suggest that the honey badger forms monogamous pairs (Estes, 1992; Mendelssohn & Yom-Tov, 1999; Johnson *et al.*, 2000).

It is further predicted that individuals will either share space by temporally avoiding one another or by controlling access to shared resources through dominance (Hornocker *et al.*, 1983; Sandell, 1989; Minta, 1993). Without parental obligations males can invest heavily in mating (Emlen & Oring, 1977), and this is likely to result in intense competition for receptive females. While mate choice and direct male-male competition (usually involving conspicuous combat and/or aggressive display) are the most common mechanisms of sexual selection (Clutton-Brock *et al.*, 1979), less obvious behaviours (review: Andersson & Iwasa, 1996) such as searching ability (Schwagmeyer, 1988), endurance rivalry (ability to remain reproductively active during a large part of the season; Andersson & Iwasa, 1996), sexual coercion (Clutton-Brock & Parker, 1995), sperm competition (mate guarding, frequent copulation and the ability to displace rival sperm i.e. large testes; Andersson & Iwasa, 1996) and infanticide (Andersson & Iwasa, 1996) might also be involved.

The open Kalahari landscape and the potential to habituate and follow selected individuals provided a unique opportunity to observe and describe intraspecific interactions in the honey badger. This chapter provides the first insight into the breeding system of the honey badger with information on the form and duration of parental care and pair bonds, reproduction, the number of mates, form of courtship, coercion and competition and the extent of mate choice. In addition, data on life history variables are presented (as per Gittleman, 1986; Johnson *et al.*, 2000), to correct previously contradictory information and to enable comparison with other species and breeding systems.

7.3 Study area & Methods

7.3.1 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 KTP, which is characterized by medium to high dunes on reddish sands where *Acacia haemotoxlon* appears in a shrublike form with scattered *Boscia albitrunca* trees (Van Rooyen *et al.*, 1984).

7.3.2 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 at the capture site. 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. Detailed information on the techniques of capture, marking and immobilization are provided in Appendix A.

The mass and linear dimensions (body length, shoulder height, neck circumference, testes) of all captured animals were measured (Chapter 2) and physical features of each animal e.g. ectoparasites, scars and wounds were recorded. Honey badgers were broadly divided into four 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). These age classes are presented in detail in Appendix A.

Nine radio-marked adult badgers (five females with five cubs and four males) were habituated to the vehicle and direct continuous observations of habituated individuals ranged from one to twelve days ($\bar{x} = 4$ days, n = 91) with an additional 57 short observation periods (less than 24 hours) ranging from 45 min to 20 h (5811 h in total). Selected activities were timed and described, and where possible interactions between individuals were filmed (16 mm) and photographed for closer examination.

The life history variables described in this study are based on those used by Gittleman (1986) and Johnson *et al.* (2000) and were estimated as follows:

- Litter size: average number of offspring at birth, estimated from the number of young carried to new den after 2 - 5 days.
- Gestation length in days: average time from conception estimated from time of oestrus or mating activity, to birth estimated when a female reused a burrow for > 2 days.
- Weaning age and lactation period in days: length of time from birth to independence from maternal milk, estimated as time from birth to when females were observed taking prey items back to the den.
- Age of independence: age when cub is independent of parental care (i.e. foraging independence; Bekoff *et al.*, 1984) estimated from visual observations.
- Inter-birth interval / litters per year: period between successive births (months) for individual females.
- Time to sexual maturity in months: estimated as the age at which individuals were observed to mate.

The following dichotomous or ordinal variables were also assessed as per Johnson *et al.* (2000): seasonal breeding (yes / no), social class (solitary, pairs, variable groups or groups) and delayed implantation (yes / no).

Testes weights were calculated indirectly from captured study animals by using the formula:

weight (g) = 2 x volume of a single testes (cm ^{3}) x 1.1 (Harcourt *et al.*, 1995)

Testicular volumes were calculated using the formula for an ellipsoid:

$$4/3 \times \Pi \times L/2 \times b/2 \times h/2$$

where L, b and h are the length, breadth and height of the testes measured in centimetres (Rose *et al.*, 1997). Actual fresh weights of testes from five honey badgers were obtained from the record cards of Bulawayo Natural History Museum specimens (Collector: R. Smithers; Museum No's: 66005; 26590; 26817; A31; 32826) and were used for comparison. For comparison with other mammals, testes weight (g) was calculated as a percentage of the average body mass of adult males (g) and as relative testes weight i.e. the ratio of observed testes size to the testes size, as predicted by $Y = 0.035X^{0.72}$ where X is observed body mass (Kenagy & Trombulak, 1986). Statistical tests follow Zar (1999) and are indicated in the text.

7.4 Results

7.4.1 Life history characteristics

7.4.1.1 Reproduction

The data confirm that the honey badger is a solitary carnivore i.e. adults do not cooperate in cub rearing, foraging, or territory defense. In all cases only a single cub (n = 20; six females, eight males, four unknown sex) emerged from the burrow after a gestation of approximately 50 - 70 days (n = 4). Males were not involved in parental care.

Cubs were born throughout the year (n = 17; Table 7.1) and female reproduction is therefore considered asynchronous, although there were more births in the hot-wet season (January-April; 47 %) and hot dry season (September-December; 35 %) than the cold dry season (May-July; 18 %). This trend is supported by the timing of mating interactions with the majority observed in the hot-dry season (66 %, n = 8), with the cold-dry season intermediate (25 %; n = 3) and only a single observation of mating in the hot-wet season.

The length of the oestrus cycle is not known, but behavioural indications of oestrus (latrine visits by females: Chapter 6) suggest that females are in oestrus or attractive to males for a minimum of two weeks.

7.4.1.2 Cub development

Den cubs (0 - 3 months old) were never captured as they remained in the den whilst their mothers went foraging, but they were observed being carried from one den to another in the mother's mouth (not on the back as suggested by Ranjitsinh, 1982). In the early stages of development cubs were almost hairless and only attained the characteristic black and white pelage at 3 - 5 weeks old (n = 2). Suckling occurred in the den and was only seen above ground on one occasion when the female was moving to a new den. The suckling position was unusual as the mother lay on her back, placed the cub on her belly with his tail near her head, and clasped her forearms around him. At 2 - 3 months of age the cubs (n = 5) accompanied their mothers foraging and females reverted to the typical pattern of sleeping in a different hole each night. Females carried prey items back to the den from two months onwards and weaning is thus assumed to occur between 2 - 3 months. Cub development was slow, and juveniles remained with their mothers for at least 12 – 16 months (n = 7; Table 8.1) before independence. For the first 12 months they were entirely dependent on their mothers for food, with a gradual increase in hunting and digging proficiency until just prior to independence when they were able to catch prey items on their own.

Age of sexual maturity in males remains unknown, but the increase in testes size and mass after independence, the late dispersal of male cubs (Chapter 5) and the behaviour of older ependence, the late dispersal of male cubs (Chapter 5) and the behaviour of older males towards young males (section 7.4.3) suggests that young males are not sexually mature on independence and only reach maturity at 2 - 3 years old. Age of sexual maturity in females is also unknown, but unlike males they disperse immediately on independence (Chapter 5) and reach adult weight before independence. In many carnivores, including European badgers *Meles meles,* dispersal occurs in sexually mature animals (Cheeseman *et al.*, 1988) suggesting that female honey badgers might be sexually mature on independence at 12-16 months. In the similarly sized river otter *Lutra canadensis* and Eurasian otters *L. lutra* both sexes reached sexual maturity in their second year (Kruuk, 1995).

As a result of the long time to independence, birth intervals were longer than 12 months and females did not breed every year. The trigger for independence remains unclear but appears to be either the presence of males during mating (n = 2) or the birth of the next cub (n = 2). While sample sizes were small there was no difference in the mean age to independence in male (14.5 months; n = 6) and female cubs (14.6; n = 3) despite large differences in body size at independence. On one occasion a male badger (J♂33) was still with his mother when he was 22 months old. In this case the adult female was seen interacting with other males on two occasions but did not appear to have another cub. During one of these mating periods the cub separated from his mother and remained alone for 2 months before rejoining her. A male cub (Am14) weighing 8.8 kg on independence was captured a month later and found to weigh only 6.5 kg. Two months later he was found dead.

Table 7.1 Timing of births and independence of honey badger cubs in the KTP. In some cases date of birth was estimated from the size of the cub when it was first observed.

Female / Cub number	Est. Date of birth	Season	Date of independence	Minimum age at independence (mths)
A♀17 / J♀01	~ 01/96	Hot-wet	02/97	13 mths
A♀15 / J♂14	~ 01/97	Hot-dry	01/98	12 mths
A♀16 / J♀10	~ 01/97	Hot-wet	02/04/98	15 mths
A♀16 / J♂27	06-07/04/98	Hot-wet	-	Dead (predation)
A♀20 / J♂21	~12/96	Hot-wet	-	Dead (infanticide)
A♀20 / J♀35	16-18/05/98	Cold-dry	25/09/99	16 mths
A♀25 / J♂26	~09/97	Hot-dry	10/98	13 mths
A♀25 / J-37	24-27/11/98	Hot-dry	-	Dead (unknown)
A♀25 / J♀44	~04/99	Hot-wet	-	Still dependent 7/12/99; 8 mths
A♀30 / J♂29	~09/97	Hot-dry	10/98-12/98	13-15 mths
A♀30 / J-45	03-07/05/99	Cold-dry	-	Dead (predation)
A♀31 / J♂32	~07/97	Cold-dry	09/98-10/98	14-15 mths
A♀31 / J♀40	~12/98	Hot-wet	-	Dead (predation)
A♀34 / J♂33	~02/98	Hot-wet	-	Still dependent 17/12/99, 22 mths
A♀38 / J♀39	18-20/03/99	Hot-wet	-	Dead (starvation)
A♀38 / J-49	24- 26/10/99	Hot-dry	-	Still dependent 17/12/99, 2 mths
A♀41 / J♂41	~12/98	Hot-dry	-	Still dependent 17/12/99, 12 mths
A♀- / J-51	~ 04/97	Hot-dry	-	Dead (infanticide)

While the actual cause of death (predation or starvation) could not be determined, the period just after independence is probably a critical period for cubs. Of the 19 cubs identified, seven died, seven reached independence and four were still dependent on their mothers at the end of the study.

7.4.1.3 Mortality and lifespan

The mortality of known cubs (excluding the four cubs still dependent) was 47 %. The causes of cub mortality included starvation (n = 1 den cub), infanticide (n = 2 den cubs), predation (n = 3; 1 den cub, 2 foraging cubs) and one death of unknown causes (den cub). On two occasions mother and the cub were killed at the same time, the indications being that large predators were involved (spoor, teeth marks on radio implants).

Three of five radiomarked young males (60 %) died before reaching adult status. One was thought to have died of starvation, one became blind in one eye and was later found dead and the remains of a third were found in a hyaena den. Within the study population, adult mortality differed between males (58 %; n = 12) and females (23 %; n = 13) but this was not significant at these small sample sizes (p = 0.087; Binomial test). Interactions with predators are discussed in detail in Chapter 4 (section 4.3.2.2).

On the basis of tooth wear and physical deterioration of individuals during the study, it is predicted that honey badgers in the southern Kalahari do not live more than 7 - 9 years, possibly even less, however honey badgers are known to live up to 28 years in captivity (Tel-aviv Ramat Gan Zoological Centre, Israel; ISIS Sheets).

7.4.2 Wounds and scars

Scarring and wounding can provide a subjective index of the degree of intra- and interspecific aggression in carnivore populations, providing the injuries rarely result in death (Minta, 1993). Recent wounds and nail rake marks, considered to have been caused by other honey badgers, were found on the face, neck and upper belly of four (22 %) adult male honey badgers (Plate 7.1). Isolated small scars were also noted in 80 % of older honey badgers of both sexes but these may have been caused by skirmishes with prey or interspecific interactions with leopard *Panthera pardus*, lion *P. leo*, black backed jackal *Canis mesomelas* or Cape fox *Vulpes chama* (Chapter 4).

Of particular interest was the large scar or callus found in the middle of the back of twelve (85.7 %) of the fourteen adult male honey badgers captured. This was never seen in a female. It varied in size (70 - 182 cm^2) and structure from a thickening or callus with no associated change in hair colour to a prominent scar noticeable from a distance as a raised area of whiter hair (Plate 7.2).

There was evidence that the scar developed over time as on two occasions (Am4, Am6) adult male honey badgers showed no signs of a scar on first capture but were later (16 months and 10 months respectively) seen with prominent scars. In addition, Am24 had no sign of a scar at first capture but showed definite signs of a thickening and callus when captured 8 months later. All four of the male honey badgers (Am43, Am12, Am6, Am9) that were considered old (i.e. had excessive tooth wear, missing and rotten teeth, grey faces and dark pelage) had

Plate 7.1 Wounds on an adult scarback male (Am13) caught while interacting with other adult males around a receptive female.

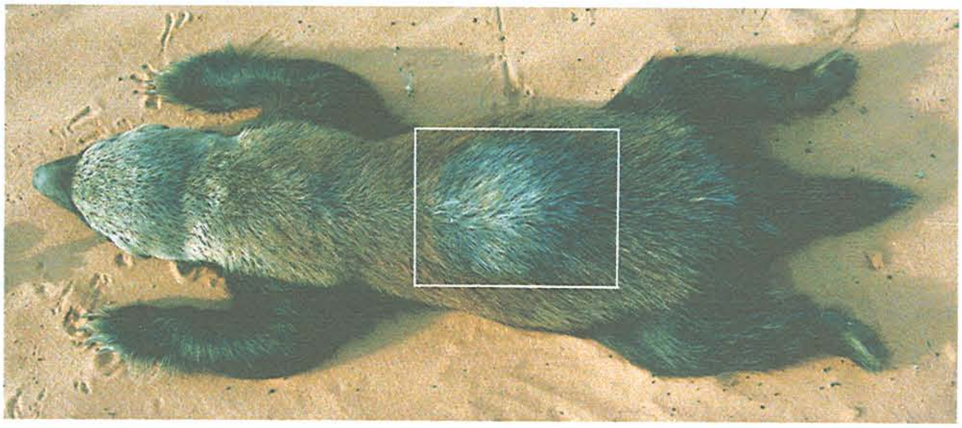

Plate 7.2 Prominent scar in the middle of the back of an adult male honey badger (Am9). The area of thickening measured 13.6 cm x 15 cm with an inner area of white hair.

prominent back scars, whilst none of the young males, females or dependent cubs showed any signs of a thickening or scar. The scar is not a regional phenomenon as it has also been identified in male honey badgers from the Western Cape, South Africa and Mana Pools National Park, Zimbabwe (K. Begg, pers. comm.), as well as on four male study skins from Botswana (Bulawayo Museum of Natural History, Zimbabwe) and one male study skin from Namibia (Amathole Musem, South Africa).

Histopathological examination of the scar revealed an area of thickened skin, irregularly bumpy with very little hair growing from it. Various sections of the affected skin were all similar and showed only large amounts of mature fibrous connective (scar tissue) in the dermis. No inflammation or glands were present and the appearance of the scar ruled out the possibility that it was due to a bacterial, fungal or parasite infection or that it was a glandular proliferation associated with hormonal changes (E. Lane, pers. comm.). While there was no indication of how it occurred, it was considered unlikely that it was caused by a single event, as the scar was a long-standing abnormality. Its presence in only male honey badgers and the development of the scar over time suggest that it is due to intraspecific interactions and may be the result of repeated bites on the same area over time. Captive animals in the Johannesburg Zoo, South Africa do not show any signs of a scar or callus although males and females are in the same enclosure (pers. obs). This may suggest that scar formation is due to male-male interactions during competition for females.

7.4.3 Male-male interactions

Intraspecific interactions included both male-male (n = 118; Table 7.2) and intersexual interactions (n = 35) but on no occasion were two adult females seen together. Male interactions were of two types: associations (n = 33) where groups of two or more male honey badgers were observed travelling together and paired interactions (n = 85), which were direct encounters between two individuals (Table 7.2). Paired interactions between male honey badgers were further divided into three categories: aggressive, ritualized agonistic and amicable (Ferguson, 1978; Table 7.2).

7.4.3.1 Aggressive interactions

In aggressive interactions (12 %), one individual physically attacked and chased another, and the apparent aim of the aggressor was to hurt its counterpart. Aggressive interactions involved direct bodily contact, biting, tumbling and then chasing. While aggressive interactions were rare (n = 10), they were preceded by ritualised agonistic posturing that escalated into direct aggression initiated by the aggressor. On all occasions they occurred between adult males at least one of which was a scarback adult (Table 7.3) in close proximity to a burrow, which contained a female, presumed to be in oestrus.

On all occasions when only one scarback was involved (n = 7), this individual was the aggressor. Given the assumption that the scar develops with age (section 7.4.2), the aggressor was also the older of the two honey badgers. On three occasions the aggressor was seen to bite the subordinate on the back, suggesting that repeated biting may be the cause of the back scar. Initial tumbling and biting with vocalisations lead to the dominant male chasing the other male for 0.3 - 1 km, away from the mating burrow containing the female. On two occasions, the aggressor was then seen to visit and scent mark at latrines in the vicinity before returning to the burrow, and in eight cases the aggressor scent marked (repeated squat marking, anal drag and belly rub, Chapter 6) at the burrow entrance before re-entering.

Table 7.2 Frequency and type of paired interactions and associations observed between male honey badgers in the KTP.

Type of interaction	Participants	No. of interactions (%)
1. Paired interactions (n = 85)		
a) Agonistic	Scarback vs. scarback	11 (17 %)
	Scarback vs. non scarback adult	34 (53 %)
	Scarback vs. young adult	19 (30 %)
	Overall	64 (75 % of paired inter.)
b) Aggressive	Scarback vs. scarback	3 (30 %)
	Scarback vs. non scarback adult	7 (70 %)
	Overall	10 (12 % of paired inter.)
c) Amicable	Non scarback adult vs. young adult	4 (40 %)
	Young adult vs. young adult	7 (60 %)
	Overall	11 (13 % of paired inter)
2. Associations (n = 33)		
a) Straight line walking	Unknown	6 (18 %)
	Scarback & others	22 (67 %)
	Non scarback & others	5 (15 %)

Table 7.3 Descriptions of intimidation and appeasement postures and associated vocalizations observed in male honey badgers during paired interactions in the KTP.

Behaviour	Intimidator	Appeaser
Posture	Standing tall, stiff-legged, head high.	Head and body low to the ground.
Vocalization	Short, deep grunt- rattle vocalization	High pitched, cackle and jaw smacking [1]
Tail signalling	Tail standing vertical above the body, hair erect "bottlebrush".	Tail down, hair not erect
General behaviour	Approaches subordinate slowly using stiff-legged posture. Pushes sideways with flanks touching. When subordinate is in a hole, the dominant collapses the hole entrance by digging at the side walls, until the subordinate exits.	Head low and backs off. Backs off facing the aggressor, then turns around and runs off. Subordinate exits hole, vocalising, and runs off.

[1] The sound of jaw smacking/clapping appeared to be produced by rapidly opening and closing the mouth and sounded like the honey badger was "clacking" the teeth together.

7.4.3.2 Ritualized agonistic interactions

During agonistic interactions, one individual appeared to intimidate a subordinate individual through a series of ritualised postures and vocalizations, and the subordinate reciprocated with appeasement postures and vocalisation (Table 7.3). No overt aggression was observed during these interactions and while some physical contact was observed (i.e. pushing), the intention of the contact did not appear to be to inflict bodily harm on the subordinate.

Agonistic interactions were most commonly seen between adult males (70 %) but were also observed between adult and young males (Table 7.2). On four occasions young males presented appeasement postures and vocalizations towards the adult male, but the adult males appeared to ignore them (no intimidating postures). Repeated interactions were frequently seen between the same individuals over periods of 2 - 4 days, particularly around females in oestrus and within male-male associations

7.4.3.3 Amicable and/or neutral interactions

Amicable and/or neutral interactions between males were rare (n = 11) and were identified as interactions where neither individual appeared dominant or subordinate and no aggressive, intimidation or appeasement behaviour was observed. On six occasions, males were observed foraging independently but in close proximity to each other. Four of these encounters involved two young males and on two occasions involved a young male and a non scarback adult. There are four records of two young males sharing a resting burrow and on one occasion a non scarback adult and a young male were observed to “play-wrestle” on a dune slope, after emerging from a hole where they had both been resting.

7.4.3.4 Associations

Male associations, varying from 18 min to 21 h, commonly consisted of two individuals (70.7 %), although groups of three (19.5 %) and occasionally four (7.3 %) and five (2.4 %) individuals were also observed. All associations consisted exclusively of male honey badgers, and in 81.3 % of the 27 observations where the age classes of the group members were known at least one of the males was a scarback. The behaviour of male groups containing a scar back male was distinctive and consisted of determined straight line trotting, one behind the other over long distances, latrine scent marking by all males (Chapter 6) and regular agonistic interactions (section 7.4.3.3).

The presence of unhabituated males within an association frequently precluded close observations, however, on one occasion, an association of three habituated males (adult scarback, adult no scar and young male) was observed for 14.5 h (17h07 – 07h45). All three males were in close proximity to a female presumed to be in oestrous and were observed to meet up at a latrine. While all three males scent marked at the latrine (Chapter 6; section 6.4.2.2), scent marking behaviour was interspersed by five agonistic interactions between the scarback and the non scarback with the scarback male clearly dominant. The scarback male prevented the non scarback from marking on the centre of the latrine through physical "pushing" and ritualised intimidation postures (Table 7.2; Chapter 6; section 6.4.2.2). The young male was ignored although he presented appeasement postures towards the dominant male. All three individuals left the latrine together and travelled in a straight line for ± 4 km with the non scarback in front (tail down), scarback following (tail up) and young male (tail down) at the rear, until the young male left the group. The two adult males remained together for a further 41 km actual distance (11 km straight line) of straight line trotting interspersed with 28 distinct agonistic interactions. On two occasions the non scarback caught a rodent (*Gerbillurus paeba*) above ground opportunistically, but was prevented from eating it by the scarback male who immediately ran up to him, stood tall (legs straight, hair and tail raised) and vocalized with a low rattle-growl. The non scarback male backed off the small prey item, which was then eaten by the scarback male. At 01h50 both males entered the same aardvark *Orycteropus afer* hole to rest, with regular vocalizations heard throughout the night. The following day, the males left the hole independently within 30 min. of each other and both immediately returned to the same area where the interaction had begun (11 km straight line).

7.4.4 Age and size of interacting males

Since individuals retained their intimidation or appeasement roles towards each other on subsequent encounters, these interactions suggest the presence of a dominance hierarchy. The mass, linear dimensions, age and testes size of interacting individuals were compared in an attempt to predict which individuals showed intimidation and which individuals showed appeasement behaviour.

Scar-back males were always “dominant” over non-scarback adults and young males (n = 52 interactions; 9 individuals; Table 7.2; Figure 7.1) and it is clear that the presence of a back scar in adult male honey badgers is associated with aggressive and intimidation behaviour. One scar back male (Am12) was observed to interact with two scar back adults, three non scarback adults and two young adults on repeated occasions (n = 41 interactions) and was the aggressor in each event (Figure 7.1).

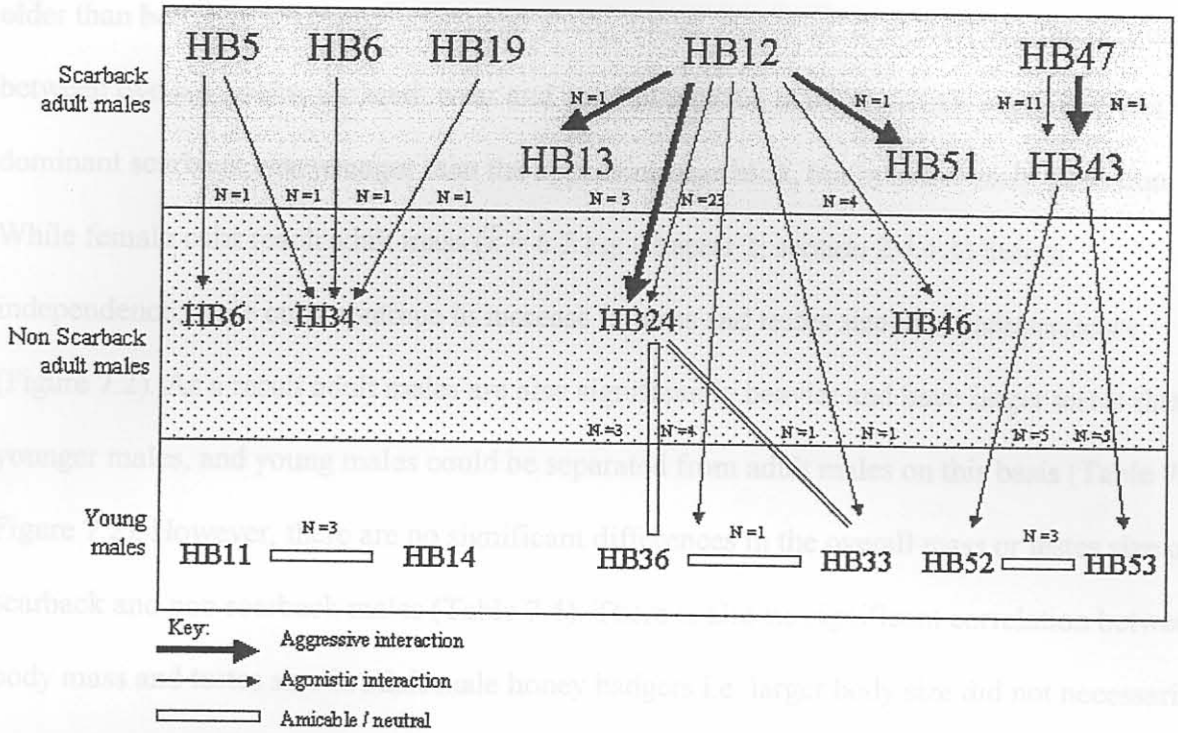

Figure 7.1 Paired aggressive, agonistic and amicable interactions observed between known male honey badgers of different age classes in the KTP. The arrows move from a dominant to a subordinate individual.

As the scar is thought to develop over time (section 7.4.2), scarback males are likely to be older than both non scarbacks adults and young adults. However, in at least one interaction between two scarbacks, the teeth wear and condition of the two individuals suggested that the dominant scarback was younger than the appeasing scar back, but in better body condition. While female cubs reach adult mass ($\bar{x} = 6.2$ kg; Chapter 2; section 2.4.4.1) before independence, male cubs continue to increase in mass and testes size after independence (Figure 7.2). As a result adult males are also significantly heavier and have larger testes than younger males, and young males could be separated from adult males on this basis (Table 7.4; Figure 7.2). However, there are no significant differences in the overall mass or testes size of scarback and non scarback males (Table 7.4). There is also no significant correlation between body mass and testes size in adult male honey badgers i.e. larger body size did not necessarily result in larger testes.

While sample sizes are small, investigation of the mass, linear dimension and testes size of each individual within unique interacting adult male pairs ($n = 8$) suggests that the dominant male tended to be heavier (75 % of interactions) and have larger testes (100 %) than the appeasing male but there is no pattern in shoulder height or body length. Overall the mean testes area of adult males known to be dominant is significantly different from the mean testes area of appeasing males (2239 mm^2 vs. 1728 mm^2; $t = 2.95$; $p < 0.05$), but there is no overall difference in the mean mass, shoulder height or body length of dominant and appeasing males. Adult male honey badgers with a mean mass of 9.1 kg are expected to have a testes weight of 24.8 g (according to the power function of Kenagy & Trombulak, 1986).

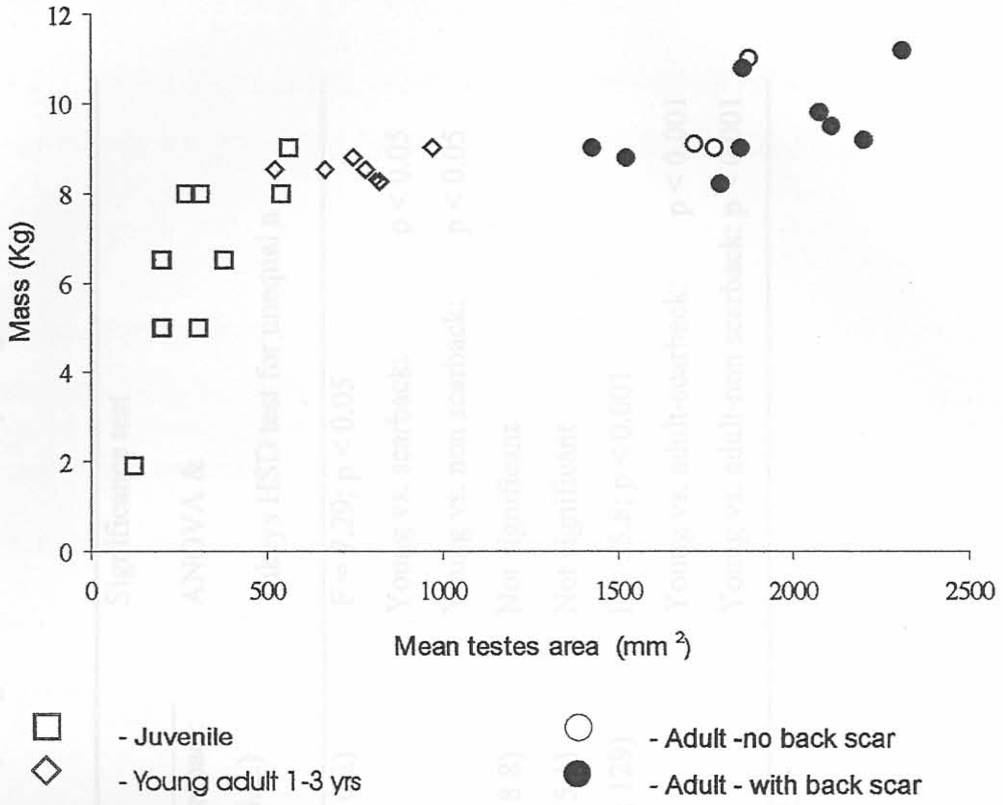

Figure 7.2 Relationship between male honey badger mass, testes area and age category, showing the increase in testes size after independence associated with a change from the young to adult male age category. Scar back males could not be distinguished from non scarbacks on the basis of testes area or mass.

Table 7.4 Comparison of the body mass, linear dimensions and testes area of young and adult male honey badgers with and without a scar in the KTP.

Dimensions	Male age class			Significance test	
	Young adult $\bar{x}$ (n; S.E.)	Adult-no scar $\bar{x}$ (n; S.E.)	Adult-scarback $\bar{x}$ (n; S.E.)	ANOVA & Tukeys HSD test for unequal n	
Mass (kg)	8.4 (5; 0.12)	9.9 (5; 0.4)	9.5 (9; 0.2)	$F = 7.29; p < 0.05$	
				Young vs. scarback:	$p < 0.05$
				Young vs. non scarback:	$p < 0.05$
Body length (mm)	920 (5; 10.8)	944 (5; 21.1)	912 (9; 8.8)	Not significant	
Shoulder height (mm)	382 (5; 8.6)	396 (5; 8.8)	401 (9; 5.1)	Not significant	
Mean testes area (mm^2)[1]	749 (5; 83.9)	1805 (4; 36)	1935 (7; 129)	$F = 35.8; p < 0.001$	
				Young vs. adult-scarback:	$p < 0.001$
				Young vs. adult-non scarback:	$p < 0.001$

---

[1] = Mean testes area = [(length$_{right}$ x breadth$_{right}$)+ (length$_{left}$ x breadth$_{left}$)] / 2.

The mean actual calculated testes weight of adult male honey badgers was twice the expected value at 54 g (n = 14; S.E. = 3.8) and is similar to the actual testes weight of museum specimens of 57 g (n = 5; S.E. = 6). On average the testes of adult male honey badgers represented 0.5 % of their mean body mass.

7.4.5 Intersexual interactions

Males and females were located together on 32 occasions. On 14 occasions spot observations of male-female pairs were observed but no further information was available, as the individuals involved were not habituated. These records include nine (28 %) observations of an adult male and female sharing a burrow and five (16 %) observations of adult pairs foraging together.

7.4.5.1 Mating /courtship

Mating and courtship behaviour was seen on 12 occasions and in all cases took place in and around a large hole. On seven occasions the male was known to have found the female by following her scent. There was some evidence of female choice as females appeared reluctant to mate with males on six occasions i.e. ran off as soon as the male arrived (n = 2); remained in the mating burrow with the male but left the burrow and ran off as soon as the male exited to chase off other males (n = 2) or tumbled and wrestled with yearling males until they moved off (n = 2; see section below). In contrast, on four occasions females were observed to "present" to males on their arrival, by backing into them with their tails raised, and on all of these occasions the male was an adult scar-back. In all cases the females were believed to be in oestrous since they had been observed to mark at latrines (section 6.4.2.2; Chapter 6) and it is considered unlikely that their reluctance to mate was simply because they were not receptive. Scar-back males were observed to mount females above ground on four occasions although it is unclear whether mating occurred. On one occasion a male mounted the female and then dragged her back into a nearby burrow.

While females displayed intimidation (dominant) behaviour when interacting with young males (Table 7.3), they presented appeasement postures (head low, backing off) and vocalizations (high pitched rattle and jaw smacking; Table 7.3) on all occasions when interacting with scar-back males. These vocalizations were frequently heard both during the meeting above ground as well as from within the mating burrow. During one typical interaction, a male scarback scentmarked at a latrine and then appeared to follow a scent trail from the latrine to a hole containing a female, vocalizing continuously with a low, short, rattle grunt. On arrival at the hole, the female emerged and backed onto the male with her tail raised. The scarback briefly smelled her genital area before mounting her while she vocalized with high pitched squeal rattle and 5 –6 jaw smacks and both then entered the hole.

On six occasions the entire (from meeting to separation) mating/ courtship interaction was observed with the female remaining in the burrow for 32 –70 hrs ($\bar{x} = 48$ hrs). If only one male was present (n = 2) both the male and female remained within the burrow for the entire period. However, on six occasions more than one male (range 1 - 4) was in attendance, and interactions between males at these gatherings varied in type (aggressive, agonistic or amicable; section 7.4.3) depending on the age and status of the individuals involved. In all cases the activity centred on access to the burrow and therefore access to the female. While young males and cubs were largely ignored even when they were in the burrow with the female, there was intense competition involving aggressive and agonistic interactions between adult males. In all mating/courtship interactions the dominant male was an adult scar back. If other adult males were in the mating burrow when the dominant male arrived (n = 2), they were ousted by the dominant male (by digging and collapsing the side walls and ceiling of the hole entrance) and chased off.

Observations of a habituated mating pair (Am12 & Af38) in the mating burrow revealed that the male physically prevented the female from leaving the burrow during a three day period by regularly pulling her backwards into the hole if she got too near the entrance and by holding her in place with his forearm when resting. Periods of intense activity accompanied by vocalisations i.e. low grunt rattle from the male and high pitched rattle and jaw clapping from the female were interspersed by periods of resting. It is assumed that multiple matings occurred during this period. A single cub was seen seven weeks later, within a week of birth.

7.4.5.2 Females and young males

On two occasions young male honey badgers approached female honey badgers and tumbling and wrestling was observed (147 & 20 min respectively). In one case the young male had found and followed the scent of the female from a latrine. While the nature of these interactions is not well understood, it was clear that the physical interaction was not overtly aggressive as neither animal appeared to be injured during the wrestling. In both observations the female was clearly dominant and it was the male that eventually moved off. Neither the male nor the female made any attempt to run off during the interaction. Examination of film footage of one interaction (D. Hughes) revealed that the female honey badger repeatedly appeared to bite the young male on the middle of the back and in the genital area during the interaction. The male did not bite the female during the interaction.

7.4.5.3 Infanticide and /or cannibalism

On two occasions an adult honey badger was recorded to kill a young honey badger cub. In the first instance (15/07/97) an adult non scarback male honey badger (Am4) arrived at a hole entrance and began digging, before entering the hole. Vocalizations were heard and a female honey badger dug herself out the back of the burrow and ran off. As she left the burrow she vocalized with a "rattle" and released scent from her anal glands, both of which are associated with the threat display towards large predators (Chapter 5). The male emerged from the same hole with a 20 cm den cub in his month seven minutes later and re-entered the main entrance where he remained for the next four hours before resuming foraging. The burrow was investigated and no cub remains were found so it was assumed that it was eaten entirely.

On the second occasion the sex of the aggressor was unknown (although the behaviour suggests a male) as the events were deciphered from the tracks by a San tracker, a day after the event. On this occasion (12/03/98) a female honey badger (Af20) was seen carrying a badly injured 3 - 4 month old cub (1.3 kg). Investigation of the tracks indicated that another honey badger had entered the den and taken the cub while the female was foraging. The female returned to the den while the other honey badger was there, and a fight ensued. The female regained possession of the cub and the other honey badger ran off, but the cub was already fatally injured (puncture wounds on forehead and left forearm, left eye damaged).

7.5 Discussion

7.5.1 Reproduction and parental care

According to the criteria defined by Creel & Macdonald (1995) the honey badger is considered to be a non-social species as there are uni-parental breeding groups and the male does not play any part in parental care. The honey badger is widely reported to show delayed implantation in common with a variety of other mustelids including the American badger *Taxidea taxus* and European badger *Meles meles* (Estes, 1992; Hancox, 1993; Johnson *et al.*, 2000). This assertion appears to be based solely on a record of two gestation periods of 153 and 162 days for captive honey badgers in Howletts Zoo, England (Johnstone-Scott, 1981). The data from the KTP do not support delayed implantation as gestation was a maximum of 50 -70 days, similar to the 62 - 72 days gestation recorded for captive honey badgers in Israel (Mendelssohn & Yom–Tov, 1999) and similarly comparable to the gestation of ten other similar sized mustelids (female mass = > 5 kg; Figure 7.3; Johnstone *et al.*, 2000). The long gestation times reported for honey badgers in captivity in England remain unexplained, but it is possible that the honey badger displays delayed implantation in the more seasonal, northern regions of its extensive distribution i.e. Turkemenia.

This study also provides no evidence for the reported litter sizes of one to four cubs ($\bar{x} = 2.5$; Neal & Cheeseman, 1996; Johnson *et al.,* 2000) as in all cases only a single cub emerged from the burrow in the KTP. While it is possible that a second cub was born but died before emergence, this is considered unlikely as females were observed to carry the cub to a new den within a few days of birth and on no occasion were females observed to move more than one cub. In captivity a litter of two was recorded on one occasion at Howletts Zoo, England (17 %; n = 6 litters), but both died within a few days (Johnstone-Scott, 1981), and once in Israel (20 %; n = 5 litters; Yom-Tov, pers. comm.). Despite an extensive literature search no records of more than two cubs could be found although the honey badger does have two pairs of inguinal mammae (pers.obs). The small litter size of the honey badger is unusual amongst other similarly sized mustelids, with the sea otter *Enhydra lutra* and the Indian smooth-coated otter *Lutrogale perspicillata* the only other mustelids recorded to have an average litter size < 2 (Figure 7.4; Johnson *et al.,* 2000). Litter sizes are variable within a species and it has been suggested that individuals living in areas with low food availability have smaller litters than those in more productive environments (Boutin, 1990; Carr & Macdonald, 1986; Geffen *et al.,* 1996). For example, litter sizes of the similarly sized Eurasian otter *L. lutra* may reach four but the mean number of cubs per litter is usually less and smaller in coastal areas (1.55 - 1.95) than in inland areas (2.3 – 2.8; Kruuk, 1995). It is therefore possible that litter sizes of two may be more common in the honey badger in more productive habitats. However, the small litter size of the honey badger in the semi-arid Kalahari was also associated with an extended period of dependence (12-16 mths) and may be a response to difficulties in provisioning more than one cub for this extended period (Oftedal & Gittleman, 1989).

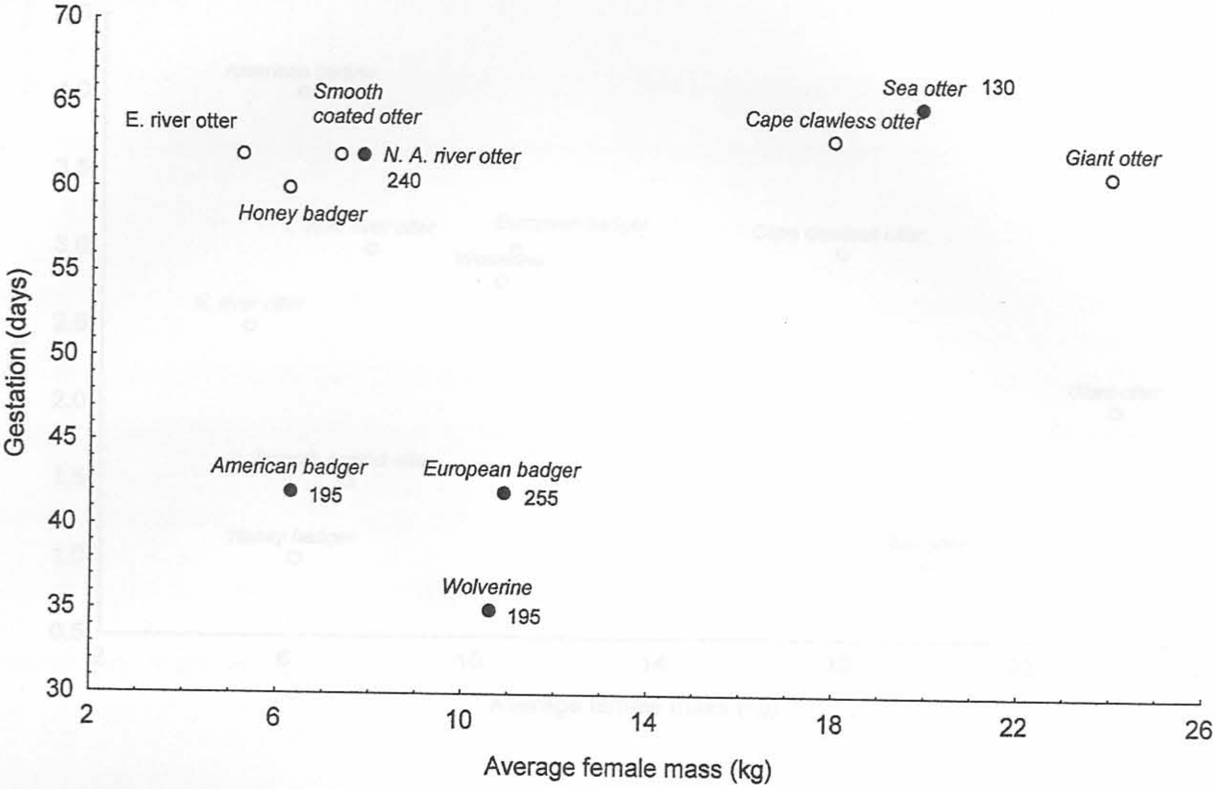

Figure 7.3 A comparison of the average length of gestation in ten medium sized mustelids (> 5 kg) with the closed circles representing those species that show delayed implantation. The length of the delay (in days) is represented by the number next to name. All data, except for the honey badger, are from Johnson *et al.* (2000).

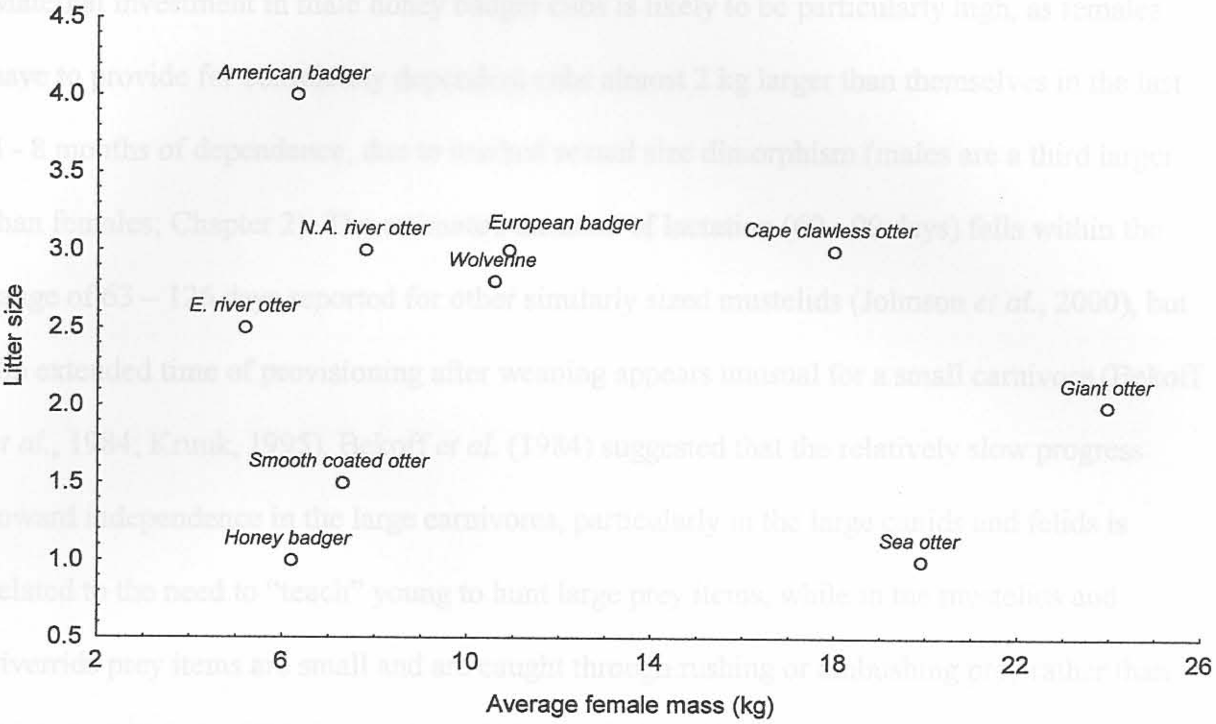

Figure 7.4 A comparison of the litter sizes of ten medium sized mustelid species (adult female mass is > 5 kg) showing the unusually smaller litter sizes of the honey badger, smooth coated otter *Lutrogale perspicillata* and sea otter *Enhydra lutris*. All data except for the honey badger are from Johnson *et al.* (2000).

Maternal investment in male honey badger cubs is likely to be particularly high, as females have to provide for completely dependent cubs almost 2 kg larger than themselves in the last 4 - 8 months of dependence, due to marked sexual size dimorphism (males are a third larger than females; Chapter 2). The estimated duration of lactation (60 - 90 days) falls within the range of 63 – 126 days reported for other similarly sized mustelids (Johnson *et al.*, 2000), but the extended time of provisioning after weaning appears unusual for a small carnivore (Bekoff *et al.*, 1984; Kruuk, 1995). Bekoff *et al.* (1984) suggested that the relatively slow progress toward independence in the large carnivores, particularly in the large canids and felids is related to the need to "teach" young to hunt large prey items, while in the mustelids and viverrids prey items are small and are caught through rushing or ambushing prey rather than through elaborate stalking procedures. However, similarly long periods of dependence (8 –12 months) have been observed in the medium sized Eurasian otter *Lutra lutra* (Kruuk, 1995) and now in the honey badger. Kruuk (1995) suggests that the unusual amount of skill required when hunting fish is likely to be the reason for the long dependence of otter cubs on provisioning by the mother. Honey badgers also require some skill to catch diverse prey, including their staple diet of gerbils (with numerous escape holes) and both poisonous and non poisonous snakes, particular since they appear to have comprised their speed for strength and digging power (Chapter 2). The long time to independence of honey badger cubs is therefore likely to be the result of a gradual development of the necessary hunting, digging and climbing skills.

The combination of only a single cub, late sexual maturity and long interbirth interval has consequences for the conservation of the honey badger, as the slow population turnover may make it more vulnerable to population extinction than other similarly sized carnivores e.g. black-backed jackal *Canis mesomelas* and caracal *Felis caracal* (Purvis *et al.*, 2001). The

Maternal investment in male honey badger cubs is likely to be particularly high, as females have to provide for completely dependent cubs almost 2 kg larger than themselves in the last 4 - 8 months of dependence, due to marked sexual size dimorphism (males are a third larger than females; Chapter 2). The estimated duration of lactation (60 - 90 days) falls within the range of 63 – 126 days reported for other similarly sized mustelids (Johnson *et al.*, 2000), but the extended time of provisioning after weaning appears unusual for a small carnivore (Bekoff *et al.*, 1984; Kruuk, 1995). Bekoff *et al.* (1984) suggested that the relatively slow progress toward independence in the large carnivores, particularly in the large canids and felids is related to the need to "teach" young to hunt large prey items, while in the mustelids and viverrids prey items are small and are caught through rushing or ambushing prey rather than through elaborate stalking procedures. However, similarly long periods of dependence (8 –12 months) have been observed in the medium sized Eurasian otter *Lutra lutra* (Kruuk, 1995) and now in the honey badger. Kruuk (1995) suggests that the unusual amount of skill required when hunting fish is likely to be the reason for the long dependence of otter cubs on provisioning by the mother. Honey badgers also require some skill to catch diverse prey, including their staple diet of gerbils (with numerous escape holes) and both poisonous and non poisonous snakes, particular since they appear to have comprised their speed for strength and digging power (Chapter 2). The long time to independence of honey badger cubs is therefore likely to be the result of a gradual development of the necessary hunting, digging and climbing skills.

The combination of only a single cub, late sexual maturity and long interbirth interval has consequences for the conservation of the honey badger, as the slow population turnover may make it more vulnerable to population extinction than other similarly sized carnivores e.g. black-backed jackal *Canis mesomelas* and caracal *Felis caracal* (Purvis *et al.*, 2001). The

Maternal investment in male honey badger cubs is likely to be particularly high, as females have to provide for completely dependent cubs almost 2 kg larger than themselves in the last 4 - 8 months of dependence, due to marked sexual size dimorphism (males are a third larger than females; Chapter 2). The estimated duration of lactation (60 - 90 days) falls within the range of 63 – 126 days reported for other similarly sized mustelids (Johnson *et al.*, 2000), but the extended time of provisioning after weaning appears unusual for a small carnivore (Bekoff *et al.*, 1984; Kruuk, 1995). Bekoff *et al.* (1984) suggested that the relatively slow progress toward independence in the large carnivores, particularly in the large canids and felids is related to the need to "teach" young to hunt large prey items, while in the mustelids and viverrids prey items are small and are caught through rushing or ambushing prey rather than through elaborate stalking procedures. However, similarly long periods of dependence (8 –12 months) have been observed in the medium sized Eurasian otter *Lutra lutra* (Kruuk, 1995) and now in the honey badger. Kruuk (1995) suggests that the unusual amount of skill required when hunting fish is likely to be the reason for the long dependence of otter cubs on provisioning by the mother. Honey badgers also require some skill to catch diverse prey, including their staple diet of gerbils (with numerous escape holes) and both poisonous and non poisonous snakes, particular since they appear to have comprised their speed for strength and digging power (Chapter 2). The long time to independence of honey badger cubs is therefore likely to be the result of a gradual development of the necessary hunting, digging and climbing skills.

The combination of only a single cub, late sexual maturity and long interbirth interval has consequences for the conservation of the honey badger, as the slow population turnover may make it more vulnerable to population extinction than other similarly sized carnivores e.g. black-backed jackal *Canis mesomelas* and caracal *Felis caracal* (Purvis *et al.*, 2001). The

Maternal investment in male honey badger cubs is likely to be particularly high, as females have to provide for completely dependent cubs almost 2 kg larger than themselves in the last 4 - 8 months of dependence, due to marked sexual size dimorphism (males are a third larger than females; Chapter 2). The estimated duration of lactation (60 - 90 days) falls within the range of 63 – 126 days reported for other similarly sized mustelids (Johnson *et al.*, 2000), but the extended time of provisioning after weaning appears unusual for a small carnivore (Bekoff *et al.*, 1984; Kruuk, 1995). Bekoff *et al.* (1984) suggested that the relatively slow progress toward independence in the large carnivores, particularly in the large canids and felids is related to the need to "teach" young to hunt large prey items, while in the mustelids and viverrids prey items are small and are caught through rushing or ambushing prey rather than through elaborate stalking procedures. However, similarly long periods of dependence (8 –12 months) have been observed in the medium sized Eurasian otter *Lutra lutra* (Kruuk, 1995) and now in the honey badger. Kruuk (1995) suggests that the unusual amount of skill required when hunting fish is likely to be the reason for the long dependence of otter cubs on provisioning by the mother. Honey badgers also require some skill to catch diverse prey, including their staple diet of gerbils (with numerous escape holes) and both poisonous and non poisonous snakes, particular since they appear to have comprised their speed for strength and digging power (Chapter 2). The long time to independence of honey badger cubs is therefore likely to be the result of a gradual development of the necessary hunting, digging and climbing skills.

The combination of only a single cub, late sexual maturity and long interbirth interval has consequences for the conservation of the honey badger, as the slow population turnover may make it more vulnerable to population extinction than other similarly sized carnivores e.g. black-backed jackal *Canis mesomelas* and caracal *Felis caracal* (Purvis *et al.*, 2001). The

honey badger is actively persecuted throughout its range and is also frequently inadvertently killed by the non selective use of poisons and gin traps (Begg, 2001; F.Cuzin, pers. comm). The honey badger appears to be unusual amongst the mustelids, as it does not have a distinct breeding season (Johnson *et al.*, 2000). This finding is supported by preliminary data from the Kruger National Park, South Africa where breeding has been recorded in February, March, June and December (Fairall, 1968). The lack of a breeding season may be a consequence of the long cub dependency, which results in a birth interval longer than 12 months (Kruuk, 1995). As a result it would be important for the honey badger to be able to reproduce at all times of the year to enable the female to begin the next gestation period after independence of the previous cub. Other sources have suggested that breeding is seasonal in other parts of its range i.e. spring births and autumn matings in Turkemenia, USSR and births timed to coincide with the maximum availability of honey in Central Africa and Nigeria (Kingdon, 1989; Hancox, 1992). However, given the lack of studies on the honey badger in other areas, this could not be confirmed.

7.5.2 Mating system

As predicted from the spacing pattern of large, overlapping male home ranges encompassing the home ranges of up to 13 females (Chapter 5), sexual size dimorphism (Chapter 2) and lack of parental care in males, the honey badger shows a polygynous mating system in the KTP in common with the majority of mustelids (Moors, 1980; Johnson *et al.*, 2000). It is possible that it is the marked size dimorphism between mothers and their still dependent male offspring that has resulted in confusion with adult male-female pairs in the past, leading to the suggestion that honey badgers form pair bonds and are monogamous (Estes, 1992; Johnson *et al.*, 2000).

In the honey badger asynchronous breeding and the long birth interval results in a skewed operational sex ratio (Emlen & Oring, 1977), with fewer receptive females than males at any time. In addition females have extensive home ranges (138 km^2; Chapter 5), and are highly mobile with no fixed den site (Chapter 5). As a result receptive females are likely to be the limiting resource for males. By adopting a roaming pattern, males are likely to achieve more matings than if they remain stationary or are territorial defending one or more females (Sandell, 1986) but they have to compete with other males for each mating opportunity. Bond & Wolff (1999) suggest two major costs for polygynous species that attempt to mate with large numbers of females; competition with other males (section 7.5.2.1) and increased predation risk. In this study, male honey badgers did appear to have higher mortality rates than females, and this may be a consequence of increased movement, activity and the use of large home ranges in males compared to females.

7.5.2.1 Intrasexual competition in males

In male honey badgers, three main forms of intrasexual competition are likely to affect their reproductive success: direct contests over oestrous females, competitive male searching and sperm competition (Schwagmeyer & Woontner, 1986; Andersson & Iwasa, 1996). Direct interactions between adult male honey badgers competing for access to the mating burrow and the receptive female commonly involve agonistic posturing and only rarely aggressive fighting and chasing. Ritualized fighting has been recognized in males of other mustelids i.e. the striped weasel *Poecilogale albnucha* , European polecat *Mustela putorius* and ferret *M. furo* (Rowe-Rowe, 1996) and is commonly accepted as a way for animals to avoid costly injury (Maynard-Smith & Parker, 1976; Ferguson, 1978; Krebs & Davies, 1987). Due to its carnivorous lifestyle (Chapter 2), the honey badger possesses formidable weaponry and there is no doubt that they could cause considerable injury to each other. Instead, adult males appear to settle most disputes through ritualized intimidation and appeasement postures. The origin and significance of the back scar in older males remains unknown. It seems probable that it is the result of intraspecific interactions, probably repeated bites in the same region over time. Some evidence exists that it is the result of male-male interactions and this is supported by the lack of a back scar in captive populations where males are kept with females but separated from each other (Johannesburg Zoo; pers comm.). Rowe-Rowe (1996) mentions that striped weasel males directed bites to those parts covered with thick, loose skin to avoid injury i.e. the lumbar region or skin of the cheeks, and it is possible that back biting in the honey badger is a form of ritualized fighting.

The predictable and consistent outcome of paired adult male interactions suggests the presence of a non linear dominance hierarchy within male honey badgers. Using game theory, Korona (1991) showed that asymmetry in age and body size are both important determinants of the outcome of a fight. However, while it is reasonable to expect that young individuals will always withdraw without a fight as they have a chance to become old, smaller individuals may not always be willing to avoid a fight otherwise they would be permanent losers (Grafen, 1987; Korona, 1991). This is largely supported in the honey badger where "winners" are usually older, but not always larger or heavier than "losers". Erlinge (1977) found a similar situation in a captive population of stoats *M. erminea*, where dominance was correlated with age and within age groups, weight was a decisive factor.

While sample sizes were small, dominance appeared to be associated with large testes. Testes size is related to the volume of interstitial tissue and hence affects the production of testosterone as well as the production of sperm. Male honey badgers with larger testes may therefore have higher testosterone levels than males with smaller testes (Woodroffe, pers comm.). While testosterone is not directly linked to increased fertility, it has been linked to social status and increased aggression (Woodroffe *et al.*, 1997). The hierarchy appears to be maintained through fairly regular direct interactions between adult males and probably also through scent marking (Chapter 7).

Since dominance is defined as "priority of access to resources that results from successful attacks, fights, chases or supplanting actions, present or past " (Morse, 1974, p. 818), it is important to determine what resources are proportioned differentially as a function of rank Dewsbury, 1982). In this case it was obvious that males were competing for access to the mating burrow and receptive females. However, the hierarchy was not an absolute system as subordinate males did gain access to the mating burrow on several occasions, either by finding the female first or by entering the hole when the dominant male left it to chase off other males.

The majority of mustelids are induced ovulators i.e. repeated or prolonged copulations are required to stimulate ovulation (Mead & Wright, 1983; Amstislavsky & Ternovskaya, 2000; Johnstone *et al.*, 2000), and it is likely that this is also true of the honey badger. The fact that females are attractive to males for a protracted period, did not leave the burrow at all during the mating period, and were physically restrained in the burrow by the males provides circumstantial evidence to support this. It might therefore not simply be access to the female that is important but rather the amount of time spent with her and the potential for repeated matings. It was impossible to compare the number of copulations of different individuals with the female, but as a result of intimidation tactics, the dominant male appeared to spend the most time in the burrow. Future genetic analysis of cub paternity will be necessary to assess whether the brief mating opportunities afforded to subordinates leads to fertilization.

While dominance, combat and aggressive display have been the major focus of research on male-male intrasexual competition (Clutton Brock *et al.*, 1979), there are other important mechanisms of sexual selection that have received much less attention. Polygynous mating systems in which the location of sexually receptive females constitutes a male's main hurdle may favour male attributes such as spatial memory, mobility and perceptiveness rather than weaponry or large size (Sandell, 1986; Schwagermeyer, 1988; Minta, 1993; Andersson & Iwasa, 1996).

If competitive searching for spatially scattered females supersedes aggressive and agonistic encounters as the primary mode of intrasexual competition in the honey badger, then the mating system may be better described as scramble competition polygyny (Schwagmeyer & Woontner, 1986; Schwagmeyer, 1988) rather than dominance polygyny or female defense polygyny. Scramble competition polygyny has been described in cervids and caprids (Owen-Smith, 1977), and ground squirrels (Schwagmeyer & Woonter, 1986) and is commonly reported among anurans and insects (Thornhill & Alcock, 1983), although it is not common within the mustelids.

In the honey badger, mobility does appear to be a prerequisite for acquiring multiple opportunities to mate, and in some cases males are able to mate without encountering any other males. Yet, the honey badger does not completely fit the scramble competition polygyny model (Schwagmeyer & Woontner, 1986) as on other occasions mating opportunities are curtailed by overt conflict over access to receptive females and the ability of some males to dominate competitors does appear to confer advantages (access to the mating burrow) in acquiring mates. This may be due to asynchronous breeding, as it has been suggested that overt conflict will diminish in populations with a combination of scattered females and oestrous synchrony (Schwagmeyer, 1988). Results from stoats (Erlinge & Sandell, 1986) and American badgers (Minta, 1993) show that while the typical mustelid pattern of intrasexual territoriality is found during the non-breeding season in these species, a system of overlap promiscuity emerges during the mating season in response to sparsely scattered females.

A third possible mechanism for sexual selection in honey badgers is sperm competition, which involves traits such as mate guarding, frequent copulation, sequestering, and production of abundant sperm to out compete other males (Andersson & Iwasa, 1996). The evolution of large testes in relation to body weight has been linked to sperm competition and multiple female matings in primates (Harcourt *et al.*, 1981); other eutherian mammals (Kenagy & Trombulak, 1986); monotremes and marsupials (Rose *et al.*, 1997) and birds (Birkhead & Moller, 1995 in Rose *et al.*, 1997). Adult male honey badgers have testes two times larger than expected given their body size, with 0.5 % of their body mass allocated to testicular tissue (Kenagy & Trombulak (1986). For comparison, average testes mass of the similarly sized European badger is 14.4 g (Kenagy & Trombulak, 1986) compared to 54 g in the honey badger. The large relative testes weight of honey badgers therefore suggests sperm competition in males and polyandry in females. This is supported by the spacing pattern of overlapping male home ranges such that more than one male has access to a particular female. In addition more than one adult male was observed to enter the mating burrow with the receptive female during a single receptive period. This has also been supported in other mustelids, for instance recent DNA analysis and visual observations have confirmed that in European badgers more than one male might mate with a sow during a single oestrus (Evans *et al.*, 1989; Christian, 1995). Multiple matings in females are associated with male counter adaptations such as mate guarding, genital structure and testes size (Reynolds, 1996).

Finally, infanticide (the killing of young animals by conspecifics) and coercion of females by males might also be important. Infanticide has been observed in many mammalian species, most notably non human primates, social carnivores and rodents (Breden & Hausfater, 1990;

Packer & Pusey, 1984). Potential adaptive explanations for infanticide relevant to honey badgers include the nutritive benefits from cannibalism (Lewison, 1998; Soltis *et al.*, 2000) and the sexual selection hypothesis, where an infanticidal individual obtains mating opportunities by killing offspring of other males and as a result increases his own reproductive success (Hrdy, 1979; Breden & Hausfater, 1990; Packer & Pusey, 1984; Lewison, 1998). Infanticide has been confirmed as a reproductive strategy in African lions and possibly tigers (Packer & Pusey, 1984). While there have been several cases of possible infanticide by female European badgers *Meles meles* (Neal & Cheeseman, 1996; Lups & Roper, 1990), no other records of infanticide by male mustelids were found. In the honey badger, the infanticidal male did not remain in the area after killing the cub, and since males were not territorial but competed for each mating opportunity, he did not retain exclusive rights to the female. It therefore seems unlikely that infanticide was a reproductive strategy. It may simply be an example of cannibalism. There was also no strong evidence for sexual coercion through physical restraint, harassment or intimidation of females by males (Clutton Brock & Parker, 1995) although females did display submissive behaviors towards dominant males during mating and courtship and were physically restrained in the burrow during mating.

7.5.2.2 Female choice

Differences in male copulatory behaviour may also result from female choice rather than strictly as a result of male-male competition (Dewsbury, 1982). Visual observations did provide some evidence for female choice as females in oestrus seemed reluctant to mate with some males but favoured other males by actively following their scent from latrines, presenting to them when they arrived (approaching males backwards with the tail up) and by making little attempt to leave the mating burrow.

It is generally thought that winners of male-male competitions are of superior quality and it would be in the female's interest to mate with these males (Korona, 1991). Thus dominance, or traits reflecting it i.e. larger size, heavy weaponry or intensive signals of fighting ability, may be important cues in female choice (but see Qvarnstrőm & Forsgren, 1998), and certainly in this study females were seen to actively present to dominant males. It addition it is possible that just as males assess the dominance ranking of other males through scent marking frequency and scent matching during later interactions, females use latrine visits for a similar function i.e. to assess the dominance status of males in the area and later match the scent found at latrines with males that approach her for mating (Chapter 6).

7.5.3 Sexual size dimorphism

The honey badger shows marked sexual size dimorphism with males at least a third larger than females with no overlap (Chapter 2). Moors (1980) provided two hypothesis for the selective advantages of size dimorphism in mustelids; the first suggests that it reduces intersexual competition for food by enabling the sexes to exploit different prey; the second suggests that in polygynous species the large size of males is due to sexual selection either through male-male competition or female choice (Weckerley, 1998). Detailed analysis of diet and feeding behaviour of honey badgers in the southern Kalahari provided little evidence for the first hypothesis (Chapter 2). During direct interactions heavier males were frequently dominant over lighter males but there was no significant pattern in linear dimensions (body length and shoulder height). However, as mentioned previously, sexual selection may also operate through non-aggressive searching and mate guarding (Andersson & Iwasa, 1996; Schwagmeyer, 1988; Minta, 1993), and larger size may confer an advantage to a male by increasing his mobility (longer legs) and therefore increase his ability to scent mark and search for receptive females throughout his extensive home range ($\bar{x} = 548$ km^2). In addition large size may increase a male's success at sequestering a female in a mating hole. There is therefore some evidence to support the hypothesis that size dimorphism in the honey badger is primarily the result of sexual selection.

7.6 References

ACOCKS, J.P.H. (1988) Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa* **57**.

AMISTISLAVSKY, S. & TERNOVSKAYA. Y. (2000) Reproduction in mustelids. *Animal Repro.Science* **60-61,** 571-581.

ANDERSSON, M. & IWASA, Y. (1996) Sexual selection. *Trends in Ecol. & Evol.* **11,** 53-58.

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

BEGG, K.S. (2001) Report on the conflict between beekeepers and honey badgers Mellivora capensis, with reference to their conservation status and distribution in South Africa. Published to www.honeybadger.com Unpublished report for the Endangered Wildlife Trust, Johannesburg.

BEKOFF, M., DANIELS, T.J. & GITTLEMAN, J.L. (1984) Life history patterns and the comparative social ecology of carnivores. *Ann. Rev. Ecol. Syst.* **15,** 191-232.

BOND, M.L. & WOLFF, J.O. (1999) Does access to females or competition maong males limit male home-range size in a promiscuous rodent? *J. Mammal* **80**, 1243-1250.

BOUTIN, S. (1990) Food supplementation experiments with terrestrial vertebrates: pattern, problems and the future. *Can. J. Zool.* **68,** 203-220.

BREDEN, F. & HAUSFATER, G. (1990) Selection within and between social groups for infanticide. *Am. Nat.* **136**, 673-688.

CARR, G.M. & MACDONALD, D.W. (1986) The sociality of solitary foragers: a model based on resource dispersion. *Anim. Behav.* **34,** 1540-1549.

CHEESEMAN, C.L., CRESSWELL, W.J., HARRIS, S. & MALLINSON, P.J. (1988) Comparison of dispersal and other movements in two badger (*Meles meles*) populations. *Mammal. Rev*. **18**, 51-59.

CHRISTIAN, S.F. (1995) Observations of extra group mating and mate defense behaviour in badgers, *Meles meles*. *J. Zool. (Lond.)* **237**, 668-670.

CLUTTON-BROCK, T.H. (1989) Mammalian mating systems. *Proc. R. Soc. B*. **236**, 339-372

CLUTTON-BROCK, T.H., ALBON, S., GIBSON, R. & GUINESS, F. (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav*. **27**, 211-225.

CLUTTON-BROCK, T.H. & PARKER, G.A. (1995) Sexual coercion in animal societies. *Animal Behaviour* **49,** 1345-1365.

CREEL, S. & MACDONALD, D.W. (1995) Sociality, group size and reproductive suppression among carnivores. *Ad. study of behaviour* **24**, 203-257.

CUZIN, F. (1996) Répartition actuelle et statut des grands Mammifères sauvages du Maroc (Primates, Carnivores, Artiodactyles). *Mammalia* **60**, 101-124.

DEWSBURY, D.A. (1982). Dominance rank, copulatory behaviour and differential reproduction. *Quart. Rev. Biol*. **57,** 135-159.

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.

ERLINGE, S. (1977) Agonistic behaviour and dominance in stoat (*Mustela erminea* L.) *Z. Tierpsychol*. **44,** 375-388.

ESTES, R.D. (1992) *Behaviour guide to African mammals*. University of California Press, Los Angeles.

EVANS, P.G.H., MACDONALD, D.W. & CHEESEMAN, C.L. (1989) Social structure of the Eurasian badger (*Meles meles*): genetic evidence. *J. Zool,(Lond.)* **218,** 587-595.

FAIRALL, N. (1968) Reproductive seasons of some mammals in the Kruger National Park. *Zool. Afric.* **3,** 189-210.

FERGUSON, J.W.H. (1978) Social interactions of black-backed jackals *Canis mesomelas* in the Kalahari Gemsbok National Park. *Koedoe* **21**, 151-162.

GEFFEN, E., GOMPPER, M.E., GITTLEMAN, J.L., LUH, H., MACDONALD, D.W. & WAYNE, R.K. (1996) Size, life history traits and social organization in the Canidae: A re- evaluation. *Am. Nat.* **147**, 140-160.

GITTLEMAN, J.L. (1986) Carnivore life history patterns: allometric, phylogenetic and ecological associations. *Am. Nat.* **127,** 744-771.

GRAFEN, A. (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.* **35,** 462-467.

HANCOX, M. (1992). Some aspects of the distribution and breeding biology of Honey badger. *Small Carnivore Conservation* IUCN/SSC **6,** 19.

HANCOX, M. (1993) Delayed implantation in badgers and other mustelids: a review. *Mustelid & Viverrid* **8,** 14-15.

HARCOURT, A.H., HARVEY, P.H., LARSON, S.G. & SHORT, R.V. (1981) Testes weight, body weight and breeding systems in primates. *Nature* **293,** 55-57.

HARRISON, D.L. & BATES, P.J.J. (1991) *The mammals of Arabia*. Pp: 135-137. Harrison Zoological Museum Publication.

HORNOCKER, M.G., MESSICK, J.P. & MELQUIST, W.E. (1983) Spatial strategies in 3 species of Mustelidae. *Acta Zool. Fenn.* **174,** 185-188.

HRDY, S.B. (1979) Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* **1,** 13-40.

JOHNSON, D.S.P., MACDONALD, D.W. & DICKMAN, A.J. (2000) An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Review* **30**, 171-196.

JOHNSTONE-SCOTT, R. (1981). Notes on the management and breeding of the African ratel. *Proc. Symp. ABWAK/Ratel* **5,** 6-15.

KENAGY, G.J. & TROMBULAK, S.C. (1986) Size and function of mammalian testes in relation to body size. *J. Mammal*. **67**, 1-22.

KINGDON, J. (1989) *East African mammals: Carnivores*. **3A,** 87-103. University of Chicago Press, Chicago.

KORONA, R. (1991) On the role of age and body size in risky animal contests. *J. Theor. Biol.* **152**, 165-176.

KREBS, J.R. & DAVIES, N.B. (1987*) An introduction to behavioural ecology*. Blackwell Scientific Publications, Oxford.

KRUUK, H. (1989) *The social badger. Ecology and behaviour of a group living carnivore (Meles meles*). Oxford University Press, New York.

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

KRUUK, H. & MILLS, M.G.L. (1983) Notes on the food and foraging of the honey badger (*Mellivora capensis*) in the Kalahari Gemsbok National Park. *Koedoe* **26**, 153-157.

KRUUK, H.H. & PARISH, T. (1987) Changes in the size of groups and ranges of the European badger *Meles Meles*. L. in an area in Scotland. *J. Anim. Ecol.* **56,** 351-364.

LEWISON, R. (1998) Infanticide in the hippopotamus: evidence for polygynous ungulates. *Ethol. Ecol. Evol.* **10**, 277-286.

LUPS, P. & ROPER, T.J. (1990) Cannibalism in a female badger (*Meles meles*): infanticide or predation. *J. Zool. (Lond.)* **221,** 314-315.

MACDONALD, D.W. (1983) The ecology of carnivore social behaviour. *Nature* **301**, 379-384.

MAYNARD-SMITH, J. & PARKER, G.A. (1976) The logic of asymmetric contests. *Anim. Behav.* **24,** 159-175.

MEAD, R.A. & WRIGHT, P.L. (1983) Reproductive cycles of Mustelidae. *Acta. Zool. Fennica* **174,** 169-172.

MENDELSSOHN, H. & YOM-TOV, Y. (1999) *Mammals of Israel*. Israeli Academy of Science, Israel.

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

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.

MORSE, D.H. (1974) Niche breadth as a function of social dominance. *Am. Nat.* **108,** 818-830.

NEAL, E. & CHEESEMAN, C. (1996) *Badgers*. Poyser Natural History, London.

OFTEDAL, O.T. & GITTLEMAN, J.L. (1989) Patterns of energy output during reproduction in carnivores. In: *Carnivore behaviour, ecology and evolution* (Ed. J.L Gittleman). Chapman & Hall, London.

OWEN-SMITH, N. (1977) On territoriality in ungulates and an evolutionary model. *Quart Rev. Biol* **52,** 1-38.

PACKER, C & PUSEY, A.E. 1984. Intrasexual infanticide in carnivores. In: *Infanticide* (Ed. G. Hausfater & S.B. Hrdy). Alsine, New York.

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

PURVIS, A., MACE, G.M., & GITTLEMAN, J.L. (2001) Past and future carnivore extinctions: a phylogenetic perspective. In: *Carnivore Conservation* (Ed. J.L. Gittleman, S.M. Funk, D. Macdonald, D. & R. Wayne). Cambridge University Press, Cambridge.

QVARNSTRÖM, A. & FORSGREN, E. (1998) Should females prefer dominant males. *Trends Ecol. Evol.* **13**, 498-451.

RANJITSINH, M.K. (1982). Transportation of young by ratel. J. *Bombay. Nat. Hist. Soc.* **19,** 661-662.

REYNOLDS, J.D. (1996) Animal breeding systems. *Trends Ecol. Evol.* **11,** 68-72.

ROSE, R.W., NEVISON, C.M. & DIXSON, A.F. (1997) Testes weight, body weight and mating systems in marsupials and monotremes. *J. Zool. (Lond.)* **243,** 523-531.

ROWE-ROWE, D.T. (1996) Agonistic behaviour of male striped weasel. *Lammergeyer* **44,** 1-5.

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

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* (Ed. J.L Gittleman, J.L.). Chapman & Hall, London.

SCHWAGMEYER, P.L. (1988) Scramble competition polygyny in an asocial mammal: male mobility and mating success. *Am. Nat.* **131,** 885-892.

SCHWAGMEYER, P.L. & WOONTNER, S.J. (1986) Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behav. Ecol. Sociobiol.* **19,** 359-364.

SMITHERS, R.H.N. (1986) The South African Red Data Book- Terrestrial Mammals. *South African National Scientific Programmes Report* **125**, 75-76.

SOLTIS, J., THOMSEN, R., MATSUBAYASHI, K. & TAKENAKA, O. (2000) Infanticide by resident males and female counter strategies in wild Japanese macques (*Macaca fuscata*). *Behav. Ecol. Sociobiol.*, **48**, 195-202.

STASOFT, INC. (1995) *Statistica for Windows*. Tusla, Oklahoma.

THORNHILL, R. & ALCOCK, J. (1983) *The evolution of insect mating systems*. Harvard University Press, Cambridge, Mass.

VAN ROOYEN, T.H., VAN RENSBERG, THERON, G.K, & BOTHMA, J. DU P. (1984) A preliminary report on the dynamics of the vegetation of the Kalahari Gemsbok National Park. *Koedoe Suppl* **1984,** 83-102.

WECKERLEY, F.W. (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal*. **79**, 33-52.

WOODROFFE, R, MACDONALD, D.W. & CHEESEMAN, C.L. (1997) Endocrine correlates of contrasting male mating strategies in the European badger (*Meles meles*). *J. Zool. (Lond.)* **241**, 291-300.

WOODROFFE, R. & MACDONALD, D.W. (1993) Badger sociality-models of spatial grouping. *Symp. Zool. Soc. Lond.* **65,** 145-169.

ZAR, J.H. (1999) *Biostatistical analysis*. Prentice Hall, New Jersey.