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

by

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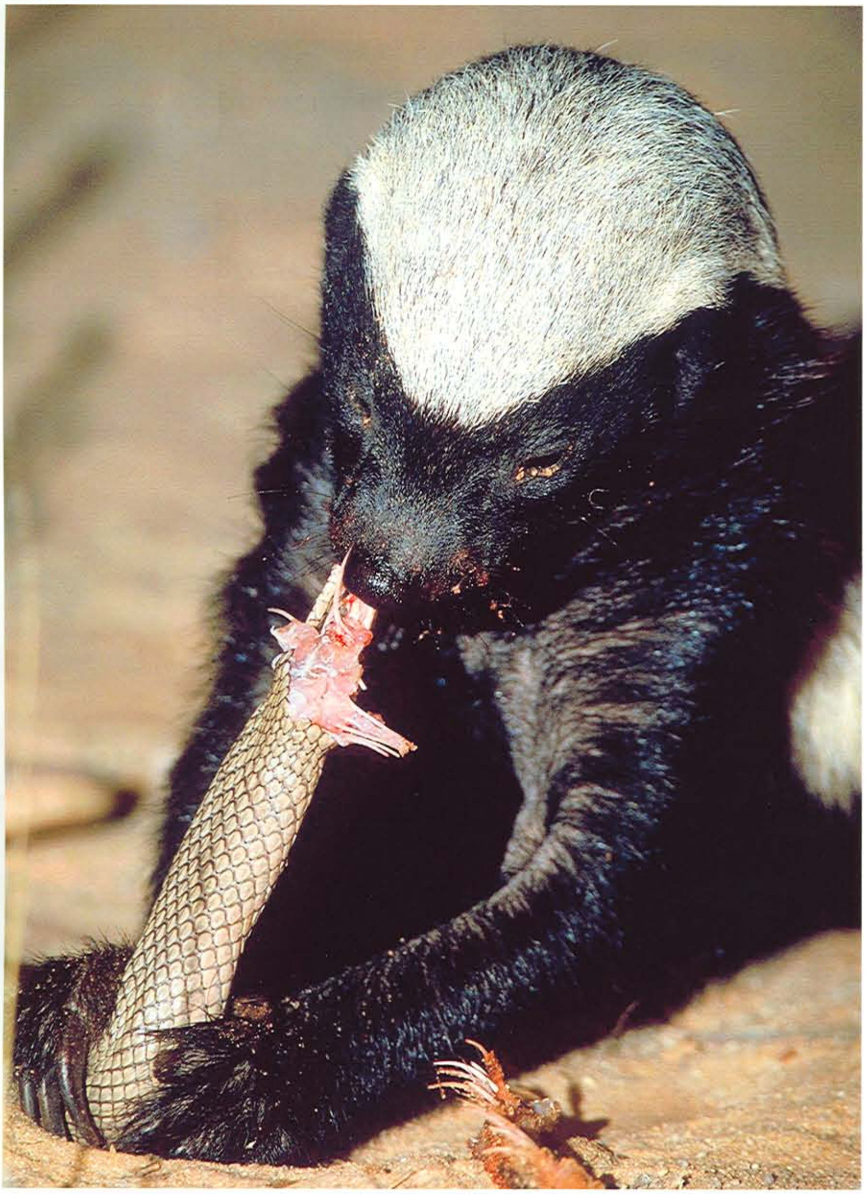
For Keith, who started it all.



Female honey badger eating a mole snake

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Summary

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

The honey badger is a solitary, generalist carnivore with strong seasonal differences in diet. In support of optimal diet theory, the cold dry season diet is characterized by low species richness, low foraging yield, high dietary diversity and increased foraging time while the reverse is true in the hot wet and hot-dry seasons. The honey badger appears to shift between alternative prey species depending on their availability on a seasonal and daily level. The daily activity patterns of both sexes show a strong seasonal shift from predominantly nocturnal activity in the hot-wet and hot-dry season to more diurnal activity in the cold-dry season and this appears to be primarily affected by temperature.

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

Interspecific interactions between the honey badger and other mammalian and avian predators were common and included intraguild predation and interspecific feeding associations between the honey badger and seven other species (two mammals; five birds). The most common foraging associations were observed between the honey badger and the pale chanting-goshawk *Melierax canorus* and black-backed jackal *Canis mesomelas*. These associations appear to be commensalism, with associating species benefiting from increased hunting opportunities and intake rate but no significant costs or benefits to the honey badger.

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General introduction

1.1 The honey badger, or ratel, *Mellivora capensis* (Schreber 1776): an overview

The honey badger has not been well studied and there is little information on all aspects of its behaviour, particularly its social organization and breeding biology. Yet the honey badger has a formidable reputation and has attracted superlatives in the popular press as "the meanest animal in the world" (Ruark, 1965), "pound for pound, the most powerful creature in Africa" (Estes, 1991) and the "bravest animal on earth" (Guinness Book of Records, 1999). Contradictory and frequently misleading accounts of the honey badger are common, both within the popular press and contemporary "field guides". An overview of the current state of knowledge of the honey badger is therefore presented here to put this study into perspective.

1.1.1 Phylogenetic relations

Originally described by Schreber as *Viverra capensis*, the generic name *Mellivora* was coined by Gottlieb Storr in 1780, the name being based on the Latin *mel* for honey and *voro,* to devour. Early common names were the honey ratel, honey weasel and in India, the honey bear (Wood, 1876).

The honey badger belongs to the family Mustelidae, which is diagnosed as a monophyletic group on the basis of the loss of the carnassial notch on the upper second molar, as well as enlarged scent glands (Wozencraft, 1989; Dragoo & Honeycutt, 1997). The mustelids have, however, been a difficult group to classify and Dragoo & Honeycutt (1997) suggest that the group is in need of systematic revision, particularly since recent molecular studies of the relationships of carnivores based on DNA hybridisation suggest that the family is polyphyletic (Bininda-Edmonds *et al.*, 1999).

Four to seven subfamilies are currently recognised (Wozencraft, 1989; Dragoo & Honeycutt, 1997; Macdonald & King, 2000). Initially, the honey badger was assigned to the sub-family Melinae because of its superficial resemblance to the true badgers (Rosevear, 1974), but in 1902, it was transferred to the Mustelinae on the basis of skull morphology and teeth. In 1912 its kinship with the wolverine *Gulo gulo* was suggested (Johnstone-Scott, 1981; Harrison & Bates, 1991). Its present position is in its own sub-family Mellivorinae, which contains a single living genus of which it is the only extant species (Wozencraft, 1989). McKenna & Bell (1997) list the genus from the Late Miocene of Europe, the Early Pliocene to Recent of Africa, and the Pliocene and Recent of Asia. Its remarkable similarities to other badgers in form suggest parallel evolution resulting from a comparable way of life (Neal & Cheeseman, 1996). Details of the early classification of honey badgers are provided by Rosevear (1974). The honey badger is one of only five mustelid species known to occur in Southern Africa, and none of these species have been well studied in the wild (Stuart, 1990).

The question of sub species has not yet been resolved. Baryshnikov (1988, 2000) recognizes two groups of subspecies; "*capensis*", which includes all the African subspecies, *M.c. wilsonii* and *M.c. pumilio* from Asia, and "*indica*" which comprises the other Asiatic forms. The African and Indian subspecies groups are distinguished on the basis of mantle colour (the presence of a whiter, border colour in the African subspecies) and skull morphometrics (the correlation of palatal length and condylobasal length; Baryshnikov, 2000). There are suggestions of up to 15 subspecies, with ten subspecies described from Africa alone, based primarily on size and pelage, mainly mantle variation (Rosevear, 1974; Baryshnikov, 2000). Since most type specimens appear to represent individual variants in a polymorphic species, and the white mantle darkens with age (Shortridge, 1934; Rosevear, 1974; pers. obs.), many of these subspecies are of doubtful validity. Genetic analysis is currently in progress (C. Matthee, Stellenbosch University, pers. comm.).

1.1.2. Geographical range and conservation status

The honey badger has an extensive range which extends through most of sub-Saharan Africa from the Cape of Good Hope, South Africa, to southern Morocco and south western Algeria, and outside of Africa through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula (Skinner & Smithers, 1990; Harrison & Bates, 1991; F. Cuzin, pers. comm.). Historically it is thought to be absent from the driest centre of the Sahara desert, the Mediterranean coast as far as the Nile Valley, and the Free State Province of South Africa (Lynch, 1983; Kingdon, 1989; Skinner & Smithers, 1990; Begg, 2001a). The distribution of the honey badger from southern Africa to India as a single species is exceptional almost rivalling that of the leopard (Rosevear, 1974). It lives in a wide variety of habitats from the dense rain forests of Zaire to the arid deserts on the outskirts of the Sahara and pro-Namib, from sea level to the afro-alpine steppes in the Bale Mountains of Ethiopia (> 4000 m; Sillero-Zubiri, 1996).

Its status in most parts of its extensive range (particularly West and Central Africa) remains uncertain, but there is little doubt that the honey badger is now absent from many areas where it previously occurred e.g. parts of Morocco (F. Cuzin pers. comm.) and parts of Israel (Ben-David, 1990), and populations may be becoming increasingly fragmented throughout its range (Smithers, 1983; Comrie -Grieg, 1985; Cuzin, 1996). Certainly in South Africa, the honey badger is now thought to be absent from large portions of the North West, Gauteng, Mpumalanga, southern Kwazulu Natal and areas of the Northern and Eastern Cape provinces (Coetzee, 1977; Pringle, 1977; Rautenbach, 1982; Smithers, 1986; Skinner & Smithers, 1990; Rowe-Rowe, 1992; Begg, 2001a).

Apart from man, the honey badger is considered the most destructive mammalian predator of honeybees in Africa and conflict between beekeepers and the honey badger has been recorded throughout their range (Hepburn & Radloff, 1998; Begg, 2001a). Outside of protected areas the honey badger is also actively persecuted by small livestock farmers (Kingdon, 1989; Begg, 2001b; F. Cuzin, pers. comm.), they are killed for traditional medicine (Cunningham & Zondi, 1991) and their pelts appear for sale in traditional markets in South Africa, Swaziland and Zimbabwe (Monadjem, 1998; Mellet pers. comm.; pers. obs.). They are also frequently inadvertently killed by the non-selective use of poisons and gin traps that are used to kill other problem animals of a similar size i.e. caracal *Felis caracal* and black-backed jackal *Canis mesomelas* (F. Cuzin, pers.comm.; Stuart, 1990; Begg, 2001b).

While the honey badger is not listed on the international red data list (IUCN, 1999), it appears on Appendix III of CITES (Ghana & Botswana; Rowe-Rowe, 1992) and is variously protected in specific countries. In South Africa the honey badger is listed as vulnerable in the South Africa Red Data Book (i.e. the species may become endangered if the causal factors for its decline continue; Smithers, 1986), and in the Cape Provinces, it is a schedule 2 protected wild animal (Anon, 1974), which means that a permit is required to kill or move any individual. It is essentially unprotected outside of game reserves and national parks in other provinces (Rowe-Rowe, 1992). The honey badger is legally protected in Israel (Anon, 1986) and Morocco (including the western Sahara) where it is considered "Near Threatened" due to the non-selective use of poison and traps (Cuzin, 1996). It is also considered endangered in Niger and rare in Saudi Arabia, but its status in other countries is unknown.

1.1.3 Fact & Fiction

The early records of the honey badger mention its predilection for honey and honeybee larvae (Anon, 1791; Wood, 1876; Lydekker & Sclater, 1894; Bryden, 1900). One contentious but often repeated tale, is that the honey badger fumigates the bee hive with secretions from its anal glands causing the bees to become moribund, thus allowing it to extract the brood and honey without being stung (Kingdon, 1989; Estes, 1991; Attenborough, 1998). Kigatiira (1984a; 1984b), in his thesis on the ecology of the honeybee writes that honey badgers "are highly ingenious animals, and can empty a hive at night by repeatedly holding their tail in front of the hive entrance. The bees are disturbed when this happens and attach themselves to its tail, whereupon the badger transports them some distance from the hive, and returns to carry off the unguarded honey and combs". There are however, reports of honey badgers being stung to death by honeybees, particularly when caught in apiary traps (Kingdon, 1989; Begg, 2001a).

In 1785, the Swedish naturalist, Sparrman (1786; in Friedmann, 1954) recorded native accounts of the greater honey guide *Indicator indicator* not only leading men, but also the honey badger, to beehives. This association was referred to in the early descriptions of the honey badger (Anon, 1791; Bryden, 1900; Lydekker, 1917) and has become firmly entrenched in popular texts on ornithology and natural history as an example of coevolved mutualism between birds and mammals (Estes, 1991; Attenborough, 1998). The association has recently been disputed as a myth by some ornithologists, primarily due to a lack of scientific evidence (Dean, 1985; Dean & Macdonald, 1981; Dean *et al.*, 1990; Macdonald, 1994). Yet other foraging associations between the honey badger and the pale chanting goshawk and the black-backed jackal have been widely reported (Cooper, 1974; Lombard, 1989; Mills *et al.*, 1984; Nelson & Nelson, 1987; Paxton, 1988; Borello & Borello, 1986), although the exact nature of this association remains unclear.

Some of the early descriptions commented on the honey badger's loose skin, aggression, and tenacity (Wood, 1876; Bryden, 1900; Pocock, 1920; Skaife, 1920). It has gained an undesirable reputation as a "gravedigger" in India and among the Bedouin tribes due to the belief that it digs up newly interred corpses (Wood, 1876; Blanford, 1891; Lydekker &

Sclater, 1894). In 1935 there was an intense unresolved debate of letters in the Journal of the Bombay Natural History Society about whether this reputation was deserved, as there were few verifiable accounts of exhumation (Champion, 1935, 1936; Clifford-Hurst, 1935; Dunbar & Brander, 1936; Toogood, 1936). Today, the honey badger is still regularly seen in some Muslim cemeteries in India where the dead are simply wrapped in a shroud and buried in shallow graves (M. Jones, pers. comm.). It remains to be verified whether they are actually digging up corpses or are simply eating the beetle larvae that are common in these gravesites (M. Jones, pers. comm.).

In 1947 Stevenson- Hamilton added to the increasingly formidable reputation of the honey badger by reporting that it regularly killed ungulates (buffalo *Syncerus caffer*, waterbuck *Kobus ellipsiprymnus* and wildebeest *Connochaetes taurinus*) by castration and the resulting fatal haemorrhage (Stevenson-Hamilton, 1947). By the 1960's this had become a common feature of species accounts, and the naturalist, George Sweeney (1969 in Johnstone-Scott, 1981) took it a step further by recounting the story of four tribesmen who encountered a honey badger which "hamstrung one of the men, clawed another and castrated him with one clean bite". Some species accounts were then extended to include warnings that "it will attack a human adversary in the same way, swarming up the legs and, it is said, very often attempting to attack the genital organs" (Astley Maberley, 1963; pp 227). Although frequently recounted, no recent (post 1950) or first hand accounts of honey badgers castrating animals (or man) are available, strongly suggesting that this is a myth.

Pocock (1920) and Rosevear (1974) provided detailed descriptions of the external and skeletal structure of the honey badger. The bold, black and white pattern is thought to be aposematic colouring which, with the release of a potent smell from the anal scent glands provides a warning to potential predators (Pocock, 1920; Kingdon, 1989; Ortolani & Caro, 1989). Yet while they are commonly reported to have no enemies aside from man (Smithers, 1983; Estes, 1991), there are reliable published accounts of honey badgers being killed by large mammalian carnivores (Turnbull-Kemp, 1967; Bailey, 1993; Pienaar, 1964). Eaton (1976) suggested that the these defensive attributes and the warning colouration have resulted in Batesian mimicry by infant cheetah *Acinonyx jubatus* of adult honey badgers. The long, white hair sported by cheetah cubs on their backs might mimic the appearance of honey badger adults from above and thus protect the cheetah cubs from predation, especially by raptors. This is difficult to prove, but certainly no records of large adult raptors predating a honey badger could be found, although Erwee (1988) observed an immature martial eagle *Polemaetus bellicosus* harassing a digging honey badger for 30 min before flying off.

Information from field guides and anecdotal accounts (Kingdon, 1989; Harrison & Bates, 1991; Dragesco-Joffe, 1993; F. Cuzin, *in litt* 2001) as well as stomach analysis (Stuart, 1981; Skinner & Smithers, 1990) suggest that the honey badger is a generalist, opportunistic predator taking a wide range of prey with strong regional differences in diet. Attenborough (1998) suggests that at certain times of the year the honey badger lives on little other than honey and bee grubs, while Hancox (1992) suggested that in central Africa honey badger births coincide with the maximum availability of honey. Yet honey brood only represented 14 % of the food items in the stomachs of seven badgers from Zimbabwe and Botswana (Smithers, 1983).

There have only been two previous field studies of the honey badger (Kruuk & Mills, 1983; Begg, 1995) and both were of short duration. A six-week study by Kruuk & Mills (1983) in the southern Kalahari provided preliminary information on the diet and foraging behaviour of individual honey badgers from faecal analysis and spoor tracking. They suggested that the honey badger might show sexual differences in the foraging strategy with males long distance foragers taking large prey and females short distance foragers eating smaller prey items. In a recent preliminary study in Mana Pools National Park, Zimbabwe, Begg (1995) observed groups of up to five individuals interacting, suggesting that the honey badger may be more social than previously suspected.

Detailed accounts of tame honey badgers (Sikes, 1964; Black, 1988) provided information on cub development and the first indications that scent marking was an important form of communication in the honey badger. While some sources suggest that honey badgers form monogamous pairs (Estes, 1991; Mendelssohn & Yom-Tov, 1999), it has also been suggested that they are polygynous in common with most other mustelids (Kingdon, 1989).

Little is known of the honey badger's reproductive biology or social organization and available data is again contradictory. Both Howletts Zoo, Bristol, England (Johnstone–Scott, 1975) and Tel Aviv University Zoo, Israel (Medelssohn & Yom Tov, 1999) have had some success at breeding honey badgers in captivity. At Howletts Zoo unusually long gestations of 153 and 162 days were recorded and Hancox (1993) suggested that the honey badger shows delayed implantation in common with several other temperate mustelids, including the similarly sized European badger *Meles meles* (Kruuk, 1989) and the American badger *Taxidea taxus* (Neal & Cheeseman, 1996). Yet in Tel Aviv University Zoo gestations of only 62 - 72 days were recorded, and there appeared to be no delayed implantation. To add to the confusion, the honey badger is commonly reported to have 1 - 4 young (Estes, 1991; Hancox, 1993; Neal & Cheeseman, 1996; Johnson *et al.*, 2000), yet in captivity, litter size was generally one with rare cases of two cubs (Johnstone-Scott, 1975; Medelssohn & Yom-Tov, 1999).

1.2 This study

1.2.1. Rationale

The lack of even fundamental biological information on the honey badger was the primary motivating factor behind the study, and in the light of its conservation status an in-depth study was considered both overdue and necessary.

Basic research on the mating system and social organization of a population relates directly to the conservation of a species (Kondeur & Deerenberg, 1997; Parker & Waite, 1997; Macdonald & King, 2000), and this in turn requires an understanding of its feeding ecology and diet (Macdonald, 1983; Kruuk, 1995). There is also little doubt that the formidable reputation of the honey badger has to some extent exacerbated its persecution as it is considered highly aggressive and dangerous to both livestock and man, and reliable information was needed to separate the fact from the myth.

On a more theoretical basis, suggestions of intersexual differences in foraging behaviour (Kruuk & Mills, 1983), social interactions in a presumed solitary species (Begg, 1995), possible delayed implantation in a tropical species (Hancox, 1993), and foraging associations with the pale chanting-goshawk and the black-backed jackal (Dean & Macdonald, 1981), all suggested that the honey badger deserved further study. Its position as the only species, within its own genus and subfamily and the uncertainty of its relationship to other mustelids invited comparisons with other large mustelids i.e. otters, other badgers and the wolverine.

The southern Kalahari was chosen as a study site since a preliminary six-week study of the food habits of honey badgers by Kruuk & Mills (1983) had already been successfully accomplished in this protected area. In addition, the sandy substrate and available skills of

Khomani-San trackers in the area provided a means of finding honey badgers and of obtaining indirect information through interpretation of tracks (Mills, 1990; Stander *et al.*, 1997). The open landscape also made it potentially possible to obtain visual observations of habituated individuals from a vehicle, even at night and, visual observations were considered crucial to gain an understanding of foraging behaviour, scent marking and intra- and interspecific interactions.

1.2.3.Objective

To describe the diet, foraging behaviour and social organization of the honey badger and to compare the behaviour of the honey badger with that of other mustelid species.

1.2.4 Key questions

Due to the lack of information on all aspects of honey badger ecology, the key questions were necessarily broad:

a) Does the honey badger show sexual size dimorphism and to what extent?

b) What does the honey badger eat and are there sexual and seasonal differences in diet and foraging behaviour?

c) How does the honey badger interact with other species in the Kalahari with particular reference to the reported foraging association with the pale chanting-goshawk *M. canorus* and black backed jackal *C. mesomelas*?

d) Does the honey badger support the typical mustelid pattern of intra-sexual territoriality (Powell, 1979)?

e) How is the spacing pattern maintained?

f) What is the mating system of the honey badger?

1.2.5. Overview of the thesis

This thesis has been written in the form of papers for publication and therefore each chapter is an independent unit, resulting in some repetition in study area and methods. Since so little information was previously available on the honey badger, the chapters frequently refer to each other and the sections have been numbered to facilitate this. The six data chapters have been arranged to answer the key questions in the order that they have been presented above. Appendix A is a detailed evaluation of the techniques of capture, marking and habituation used in the study. To standardize the appearance of the thesis, all references are in the form required for the *African Journal of Ecology*.

A variety of different techniques were used to collect data, but there is little doubt that direct visual observations of nine habituated, radio marked individuals provided the most important insights into foraging behaviour, social interactions, and scent marking behaviour despite relatively small sample sizes, as was found in hyaena studies in the same area (Mills, 1990). More indirect data collected from a larger radio marked population (25 adults) and spoor tracking were important for determining spatial requirements, movement patterns, life history variables and density.

The study is broadly divided into two parts: the feeding ecology and activity patterns (Chapters 2,3,4) of the honey badger and its social organisation and breeding (Chapter 5,6,7). The first step was to determine what the honey badger eats and how it obtains its food and this is presented in Chapter 2. On a more theoretical basis this chapter also investigates sexual and seasonal variation in diet and foraging behaviour in terms of optimal foraging theory (Pyke *et al.*, 1977). In addition, the extent of sexual size dimorphism in honey badgers is assessed and the data are examined for sexual differences in diet and foraging strategy.

Chapter 3, investigates sexual and seasonal differences in the time budgets and activity patterns of the honey badger in the southern Kalahari where it is relatively undisturbed by man. In particular, sexual differences in the amount of time spent engaged on social and foraging activities and the effects of extreme temperature and prey activity schedules on activity patterns are examined.

The relationships between sympatric predators are complex and may involve exploitative and interference competition as well as facilitation (Mills & Biggs, 1993; Creel *et al.*, 2001). Chapter 4 describes interspecific interactions between the honey badger and other predators in the southern Kalahari, particularly intraguild predation and the foraging associations between the honey badger and the black-backed jackal *C. mesomelas* and pale chanting-goshawk *M. canorus*. Negative interactions such as competition and intraguild predation can adversely affect population growth rate and energetic intake of the victim, while positive interactions e.g. foraging associations may increase population growth rate through increased energetic returns, vigilance or breeding success (Palomares & Caro, 1999; Creel *et al.*, 2001).

Chapter 5 begins the second half of the thesis with a description and analysis of the spatial organisation of the honey badger in the southern Kalahari. Age-and sex related differences in home range size and movement patterns are investigated and it is determined whether the honey badger supports the typical mustelid pattern of intrasexual territoriality with overlapping home ranges between the sexes (Powell, 1979; Moors, 1980).

The importance of scent marking in solitary mammalian carnivores has been well documented (Macdonald, 1985) and the function of scent marking has been widely debated over the last two decades (Gosling, 1982; Macdonald, 1985; Gorman & Trowbridge, 1989). In Chapter 6, the scent marking behaviour of the honey badger is described. Direct observations allowed scent marking events to be described in the environmental and behavioural contexts in which they occurred and the results are compared to predictions from hypotheses on the function of scent marking. Finally, Chapter 7 investigates the breeding system of the honey badger, and answers the question, is the honey badger polygynous? This chapter provides insight into the form and duration of parental care and pair bonds, reproduction, the number of mates, and the form of courtship. In addition, data on standard life history variables (Gittleman, 1986; Johnson *et al.*, 2000) are presented to correct previously contradictory information. Where the data permits more theoretical questions are addressed and the behaviour of the honey badger is compared to that of other mustelids.

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- Chapter 2 -

Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger *Mellivora capensis*.

2.1 Abstract

The honey badger, or ratel, *Mellivora capensis* has not been well studied despite its extensive distribution. As part of the first detailed study, visual observations of nine habituated free-living individuals (five females; four males) were used to investigate seasonal, annual and sexual differences in diet and foraging behaviour. Theory predicts that generalist predators "switch" between alternative prey species depending on which prey species are currently most abundant, and diet breadth expands in response to decreased availability of preferred food types. There were significant seasonal differences in the consumption of eight prey categories related to changes in prey availability but no seasonal differences in food intake per kilogram of body mass. As predicted the cold dry season diet was characterized by low species richness and low foraging yield but high dietary diversity, while the reverse was true in the hot-dry and hot-wet season. In accordance with the predictions, the results suggest that the honey badger maintains its intake level by food switching and varying dietary breadth. Despite marked sexual size dimorphism, male and female honey badgers showed no intersexual differences in prey size, digging success, daily food intake per unit body weight or foraging behaviour. Results do not support the hypothesis that size dimorphism is primarily an adaptation to reduce intersexual competition for food.

2.2 Introduction

The honey badger *Mellivora capensis* is found across the greater part of Africa, south of the Sahara and extending through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula (Neal, 1990; F.Cuzin, *in litt,* 2001). Despite its extensive distribution the species has not been well studied. This chapter provides an in-depth description of its diet and foraging behaviour from visual observations in the southern Kalahari, and investigates how diet varies seasonally and between the sexes. Not only is the feeding ecology of a species important for understanding its natural history, it is often the basis for understanding its social organisation (Macdonald, 1983; Kruuk, 1995) and is important for formulating conservation management strategies (Clemmons & Buchholz, 1998).

Information from field guides and anecdotal accounts (Kingdon, 1989; Harrison & Bates, 1991; Dragesco-Joffe, 1993; F. Cuzin, *in litt* 2001) throughout its range, as well as analysis of stomachs (Stuart, 1981; Skinner & Smithers, 1990) and faecal material (Kruuk & Mills, 1983), suggest that the honey badger is a generalist, opportunistic predator, that takes a wide range of prey with strong regional differences in diet.

As a generalist, it is expected that diet composition will differ seasonally as the honey badger "switches" between alternative prey species depending on which are currently the most abundant (Pyke *et al.,* 1977; Taylor, 1984). This has been found in other mustelids i.e. the Eurasian otter *Lutra lutra* (Carss *et al.,* 1998), American marten *Martes americana* (Ben David *et al.,* 1997), mink *Mustela vison* (Dunstone, 1993), polecat *Mustela putorius* (Lode, 1994) and stoat *Mustela erminea* (Erlinge, 1981; Martinoli *et al.,* 2001), but not in some populations of the European badger *Meles meles* where earthworms are the most important item in the diet despite wide seasonal fluctuations in availability and population sizes (Kruuk & Parish, 1981).

Classical optimal diet theory also predicts that diets will be more diverse during the lean seasons than during the rich seasons in response to the decreased availability of preferred food types (Perry & Pianka, 1997), enabling animals to maintain their overall energy intake and minimize a subsequent loss in body condition. Alternatively, animals might show seasonal modifications in activity and foraging behaviour to satisfy their nutritional requirements (Gittleman & Thompson, 1988; Gedir & Hudson, 2000).

Diet and foraging behaviour may also differ between individuals due to sex, reproductive status or age. On an intersexual level, sexual differences in prey preference have been observed in the stoat (Moors, 1980; Erlinge, 1981), weasel *M. nivalis* (Moors, 1980; Erlinge, 1981), polecat and mink (Birks & Dunstone, 1985). The family Mustelidae is characterized by sexual dimorphism in body size with males always larger than females, although the extent of dimorphism varies between species as well as geographically within species (Shubin & Shubin, 1975; Moors, 1980; Gliwicz, 1988) Two main theories have been suggested to account for this. The first claims that dimorphism reduces dietary overlap and intraspecific competition (Erlinge, 1981; Moors, 1980; Shine, 1989; Dayan & Simberloff, 1994), which is supported by the consistent trend for female mustelids to consume smaller prey than males (Moors, 1980). The second hypothesis suggests that male and female sizes can be attributed to different selective pressures with small females favoured over larger females because they need less energy for daily maintenance and can channel more energy into reproduction (Erlinge, 1981; Powell, 1979; Moors, 1980; Sandell, 1989), while larger males are favoured in competition for mates as a result of intrasexual selection (Chapter 8; Powell, 1979; Moors, 1980; Gittleman & Van Valkenburgh, 1997; Weckerley, 1998).

In the honey badger, the degree of sexual size dimorphism was previously unknown, but in a six-week study Kruuk & Mills (1983) observed differences in prey preference between individuals. They suggested that these differences might be related to intersexual differences in foraging strategies, with male honey badgers being long distance foragers taking larger prey, and females being short-distance foragers generally taking smaller prey items. If the data support this prediction and males and females show intra-sexual differences in diet and foraging behaviour that can be related to differences in body size, then this provides some support for the hypothesis that dimorphism reduces intersexual competition.

Given the lack of detailed information on the diet of the honey badger, the main question addressed in this chapter is: what does the honey badger eat and how does it catch its prey? On a more theoretical basis, seasonal variation in diet is investigated to assess whether the honey badger shows prey switching and an increase in diet breadth in response to changes in prey availability. Finally, sexual differences in prey type and foraging strategies are examined in the light of the niche partitioning theory of sexual size dimorphism.

2.3 Study area and methods

2.3.1 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 (KGNP), South Africa and neighbouring Gemsbok National Park, Botswana.

It is a semi desert region and is described as the western form of Kalahari thornveld with a very open savanna of *Acacia haemotoxylon, Acacia erioloba* and desert grasses (Acocks, 1988). This study was primarily conducted in the central dune area of the KGNP, which is characterized by medium to high dunes (10 – 25 m) on reddish sands where *A. haemotoxylon* appears in a shrublike form with occasional *Boscia albitrunca* and *A. erioloba* trees. Dune areas are interspersed with slightly undulating open plains areas, with similar plant composition but with no *B. albitrunca* trees, and pans and yellowish sands, which support shrub veld of *Rhigozum tricophorum* and *Monechma sp* (Van Rooyen *et al.*, 1984).

2.3.2 Climate

The study area falls between the 200 mm and 250 mm isohyets and is characterized by low, irregular annual rainfall (Mills & Retief, 1984). The variable rainfall plays a major role in the vegetation of the KTP (Leistner, 1967) and large differences in floristic composition, basal cover and density can be expected in the short and medium term (Van Rooyen, 1984). Three seasons are distinguished: the hot- wet season (HW) from Jan-Apr when the mean monthly temperature is approximately 20°C or higher and when 70 % of the rain falls; the cold-dry season (CD) from May-Aug when the mean monthly temperature is below 20°C and rainfall is rare and the hot-dry season (HD) from Sep-Dec when the monthly temperature is approximately 20°C and usually not more than 20 % of the rain falls (Mills & Retief, 1984).

The weather bureau of South Africa provided monthly rainfall records from the three tourist camps in the Kalahari Gemsbok National Park for the period of this study. As the study site lay within the central dune area equidistant from all measurement sites, a mean rainfall value was calculated for each season and each year using the data from all three camps (Table 2.1). All years of the study experienced comparatively low rainfall especially in the final year (1999; Table 2.1)

Table 2:1 Monthly rainfall records measured at three weather stations in the KTP summarized into seasonal totals (mm) for the period of study: June 1996- Dec 1999.

Weather Station	Season and year													
	HD 96	**Tot. 96**	HW 97	CD 97	HD 97	**Tot. 97**	HW 98	CD 98	HD 98	**Tot. 98**	HW 99	CD 99	HD 99	**Tot. 99**
Nossob	69	**240**	201	23	81	**305**	144	0	89	**233**	55	21	34	**109**
Mata Mata	5	**152**	5	0	12	**17**	53	0	37	**145**	16	45	57	**118**
T. Rivieren	68	**195**	52	19	7	**77**	60	4	51	**115**	47	19	32	**98**
Average	47	**196**	86	14	100	**133**	86	1	59	**164**	39	28	41	**108**

2.3.3 Data collection

Honey badger spoor was located by a Khomani-San tracker and followed 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 in this way and 25 individuals (13 females, 12 males) were radio-marked with Telonics radio-collars. A wildlife veterinarian subsequently implanted ten of the radio-marked adults (five females and five males), and three large cubs (one male, two females) with Telonics radio transmitters (Appendix A). All other honey badgers that were captured were individually marked by freeze branding (Appendix A).

All individuals were weighed and measured: body length (from tip of the nose to base of the tail, with the measurement taken over the curve of the body); shoulder height (from the top of the scapula to the end of the longest nail with the arm pulled straight); tail (base of tail to tip) and neck circumference.

Over 2000 hours were spent habituating nine radio-marked adult badgers (five females with five cubs and four males) to the vehicle until they could be followed without any obvious influence on their foraging behaviour (Appendix A). Habituation also enabled collection of information on non-habituated badgers (termed “other females” and “other males”) as the non-habituated individuals appeared to take their cue from the habituated badgers and sometimes relaxed in the presence of the vehicle. Over the course of the study 5244 h were spent with habituated badgers with an additional 564 h spent observing “other” honey badgers (Appendix B). Selected animals were followed continuously for observation periods ranging from one to twelve days ($\bar{x} = 4$, n = 91) with an additional 57 short observation periods (less than 24 h) ranging from 45 min to 20 h. During all observations honey badgers were observed from the roof of a vehicle averaging 10 - 30 m away depending on visibility and grass height. During continuous observations all activities were timed to the nearest minute with a digital stopwatch. Prey type, holes dug, and the number of prey items caught during each hunting attempt were also recorded. A 400 000 candlepower spotlight was used for night observations.

Rodent trapping was used to assess seasonal changes in the relative abundance (Ra) of small mammals. Eight trap-lines were set each season for three years (1997-1999) with three trap-lines set in dune habitat, three in open plains and two in *R. tricophorum* patches. Each trap-line consisted of 50 Sherman traps set in a cross formation (25 traps by 25 traps) where each trap was 15 m from the next. A trap-line was set for two nights and one day and traps were checked each morning and evening during the trapping period. Traps were baited with a mixture of rolled oats, peanut butter and vegetable oil when they were set and bait was replenished where necessary. All small mammals captured during a trapping period were marked with a spot of red paint before release to enable identification of recaptures, and the data from both nights were pooled. The relative abundance was expressed as the number of individuals captured per 100 trap-nights during the trapping period, and recaptures were not included in the count.

2.3.4 Analysis

2.3.4.1 Prey profitability

For the ten most common prey species caught through digging, an index of relative prey profitability was estimated as biomass yield per unit handling time where time spent digging + eating (min) was used as an index of handling time (Krebs & Davies, 1987). Prey items caught opportunistically above ground or through climbing were excluded from this analysis. It is acknowledged that total biomass is an imperfect measure of energy yield, but in the absence of digestibility studies and nutrient analyses, it is considered useful for this coarse index of profitability. All small mammals, small reptiles and large reptiles were eaten entirely, including the heads of poisonous snakes. On occasion the pincers and tail of scorpions were discarded, as were the wing feathers and talons of large raptors chicks. Larger mammals (>100 g) were frequently eaten underground in a burrow so it was impossible to consistently assess the amount eaten, however the hind feet (n = 2) and tail (n = 2) of springhare *Pedetes capensis* were found as well as small portions of skin from polecats *Ictonyx striatus*, African wild cat *Felis lybica*, bat-eared fox *Otocyon megalotis* and Cape fox *Vulpes chama* cubs. Since the uneaten portions of the larger prey items were relatively small and likely to be within the variation contained in the average biomass value used for each species (e.g. within the size difference between a large and small springhare), no attempt was made to subtract these from the biomass yield.

2.3.4.2 Seasonal and sexual differences in diet composition

Prey items from visual observations were summarized into eight food categories: solitary bee larvae *Parafidelia friesei*, insects (excluding solitary bee larvae), scorpions, small reptiles (<100 g, skinks, geckoes, agamas, lizards and small snakes), large reptiles (>100 g, exclusively large snakes); small mammals (<100 g, all rodents except for the elephant shrew *Elephantulus intufi*); large mammals (>100 g) and birds. Tsama melons were analyzed separately from other prey items since it appears they were primarily eaten for their water content (Section 2.4.1.1). Prey categories were calculated as percentage frequency i.e. number of food items eaten in each food category as a percentage of the total number of food items eaten, and percentage biomass. Biomass values for prey items were estimated from data in the literature (mammals and birds), relevant experts i.e. mass of snakes (G. Alexander, pers. comm.), scorpions (L. Prendini, pers. comm.), bird eggs (W. Tarboton, pers. comm.) and from weighing prey items in the field (small reptiles and tsama melons). The biomass of individual prey items in each prey category was summed to provide an estimate of the biomass contribution of each food category in each season.

Solitary bee larvae were considered in a category on their own as they were the only insect species taken in large numbers and were not eaten throughout the study (section 2.3.1.2). A coarse estimate of the number of larvae eaten and their biomass contribution to the diet was calculated by multiplying the time honey badgers spent digging at larval patches (56.2 h) with an estimate of the number of larvae eaten per minute. On two occasions a badger could be heard cracking open larval cases and estimates of 35 larvae/ 37 min and 80 larvae/ 94 min were obtained (mean = 0.88 larvae / min.). Since honey badgers frequently disappeared underground for long periods when digging out larvae, a foraging bout was timed to the last observed movement or sound of digging.

An index of dietary diversity for each season was calculated using Levin's formula for niche breadth, $N_B = 1 / \Sigma p_i^2$ where p_i is the proportion of observations in food category i of the diet (Erlinge, 1981; Lode, 1994), and the information-theoretic diversity measure of Brillouin, $H = (\log n! - \Sigma \log f_i!) / n$ where n is the sample size, and f_i is the number of observations in category i (Zar, 1999). Species richness simply represents the number of species eaten.

Since there are repeated measurements on the same animal over three seasons, differences in dietary composition between individuals were assessed using a generalized linear mixed model (Schall, 1991; J. Juritz, pers. comm.). Variation between individuals accounted for only 2.6 % of the total variation in diet (generalised linear mixed model) and this suggests that feeding patterns were consistent between animals. A first approximation of seasonal variation in diet was, therefore, obtained by combining data from different years for each of the three seasons hot-wet, cold-dry, and hot-dry.

Where possible parametric tests (analysis of variance, two-sample, two-sided t-tests) were used, with time proportions arcsine transformed before analyses to achieve normality (Zar, 1999). Non parametric tests (Mann-Whitney U test and Kruskal-Wallis test) were used where data were skewed and did not fit the assumption of normality, with Tukey's multiple comparisons to assess where differences lay (Zar, 1999). Spearmans rank correlation coefficient (r_s) was used to investigate relationships between prey abundance and their percentage contribution to the diet, and small mammal and small reptile consumption.

2.4 Results

2.4.1 Overall diet

From visual observations 3324 food items were identified to a food category and 83.6 % were identified to species level comprising 59 species (Table 2.2), with 42 food species recorded for females and 46 for males. Additional prey species were identified from spoor tracking (ground squirrel *Xerus inauris*, black-backed jackal *Canis mesomelas*), unsuccessful hunting attempts (aardwolf *Proteles cristatus,* slender mongoose *Galerella sanguinea,*) and visual records from other observers (tawny eagle chick *Aquila rapax,* honeybee brood and honey *Apis mellifera scutellata*: D. & C. Hughes, pers. comm., whitebacked vulture chick *Gyps africanus:* Marlow, 1983). Only 88 food items (2.5 %) could not be identified to a food category and these were excluded from further analysis.

During the study, honey badgers were twice observed to unsuccessfully attempt to break into bee hives. In addition, during the cold-dry season of 1999, D & C Hughes (pers. comm.)

observed two of the study animals (an adult female honey badger with her large cub) breaking into 13 bee hives over 37 visits to eat bee brood and honey comb. On 61 % of the visits the swarm's defense was sufficient to chase off the honey badgers.

Tsama melons *Citrullus lanatus* were the only plant species recorded in the diet (6 %), with invertebrates contributing 11 % and vertebrates the remaining 83 % spread over three classes (mammals, birds and reptiles).

2.4.1.1 Tsama melons *Citrullus lanatus*

Tsama melons have a low calorific value (30-100 KJ / 100 g; Mills, 1990; compared to an average of 894 KJ / 100 g for a mouse; Village 1990) but a moisture content of over 90 %. A sample of 20 uneaten tsamas was weighed and the diameter measured to provided a baseline regression of tsama size and mass ($R^2 = 0.83$, $y = 0.06x + 72.8$) against which a sample of 20 tsamas partially eaten by honey badgers could be compared. Results showed that on average only 45 % of the total mass of an individual tsama was ingested representing an average mass of 278 g (~ 83 - 278 KJ). In terms of energetic returns, approximately 2 – 7 tsamas are therefore equivalent to one Brant's gerbil *Tatera brantsii* (65 g).

Tsama melons seemed to be located opportunistically by the honey badger and were more frequently eaten in the cold dry season ($\chi^2 = 86.9$, $p < 0.001$) when they are also most abundant (Knight, 1989). The honey badger opened the tsama melons with its fore claws and teeth. Once opened, the honey badger scratched inside the tsama, licking up the moisture but discarding large sections of pips and flesh. This suggests that the honey badger primarily utilizes tsamas as a moisture source, in common with other carnivores and herbivores in the KTP (Mills, 1990), but they may also be important for other nutrients (Knight, 1989). Honey badgers were seen to drink water twice, once from an artificial waterhole and once from water running off tree trunks during a rainstorm. During a survey of 50 artificial waterholes (Feb – Mar 1996), honey badger tracks were only located at a waterhole on one occasion.

2.4.1.2 Invertebrates- Insects and scorpions

Insects were difficult to identify from visual observations and may have been underestimated. Solitary bee larvae *Parafidelia friesee* (identified by C. Scholtz) were the only insect species observed to be eaten in large numbers. An estimated 3000 larvae were eaten representing a biomass contribution of 1.2 % of the overall diet (Appendix C), and they were ranked 13th of the 59 species in terms of their biomass contribution. Male honey badgers were estimated to eat more solitary bee larvae than females despite similar periods of observation during 1998 (males: 996 h vs. females: 906 h) when these larvae were particularly important prey items (section 2.3.3). Four male honey badgers were observed digging for solitary bee larvae for 53.2 h (± 2809 larvae) on 81 occasions, and on one occasion two male badgers were observed digging at the same larval patch at the same time. In comparison, two female honey badgers (n = 2) were observed digging for larvae on only three brief occasions (two from spoor-tracking information, one visual observation) accounting for an estimated 0.1 % of the biomass consumed (158 larvae). The reasons for these sexual differences are unknown.

Evacuation of a 0.6 m x 0.5 m x 1 m block of sand within a larvae patch used by honey badgers, sieved layer by layer, showed that groups of 1 - 4 larvae are found in small chambers from 13 - 100 cm below the sand surface with the highest numbers found between 50 - 70 cm. Each larva is encased in a hard brown shell of approximately 20 mm in length, and each larval shell was cracked open individually by a honey badger. Larval patches used by a honey badger were identified by the presence of empty shells and extensive diggings consisting of 11 to 54 holes over areas from 30-700 m^2. Patches were found primarily in compacted soil in dune troughs where *R. tricophorum* shrubs predominated, and of the 41 larvae sites identified

51.2 % had honey badger latrines (Chapter 6) associated with them. Honey badgers would disappear underground when digging out these larvae, and they frequently slept in these holes after a foraging bout.

2.4.1.3 Vertebrates

Excluding the solitary bee larvae, the barking gecko *Ptenopus garrulous* (19 %) and hairy-footed gerbil *Gerbillurus paeba* (33 %) were the most common prey items and the only two species representing more than 10 % of the diet in percentage frequency (Appendix C). In terms of estimated biomass ingested they were less important (1.7 % and 5 % respectively; Appendix C) compared to larger but less frequently eaten prey species. Of the 13 species of small mammals (< 100 g) known to occur in KTP (Nel *et al.,* 1984), nine were visually recorded in the diet of honey badgers, with the hairy footed gerbil (n = 480; 62 % of small mammals eaten), Brant's gerbil *Tatera brantsii* (n = 218; 26 %) and striped mouse *Rhabdomys pumilio* (n = 88; 10%) the most commonly eaten small mammal prey species (Appendix C). Small mammal trapping revealed that these three species were also the most common prey species in the study area comprising 62 %, 21 % and 5 % of the small mammals caught (n = 1941) respectively, and they appeared to be eaten according to their availability.

Four species, springhare *Pedetes capensis* (22.2 %), mole snake *Pseudaspis cana* (21.4 %), puff adder *Bitis arientans* (12.5 %) and Cape cobra *Naja nivea* (10.5 %), each contributed greater than 10 %, and combined 67 %, of the total biomass consumed (Appendix C). The three large snake species were important in both female and male diets (42.1 % and 48.7 % respectively), but springhares represented 32.7 % of the biomass ingested by female badgers and only 4.2 % in males. While two other honey badgers (one male, one female) caught springhares opportunistically when they were already in burrows, a single female was responsible for 86 % (n = 25) of the springhares seen in the diet of female honey badgers (section 2.3.4). When this female is removed from the analysis due to her individual prey specialization, springhares represent only 1.8 % of the biomass consumed by females and 3 % of the overall biomass consumed by honey badgers (in contrast to 22 %).

2.4.1.4 Handling time and prey profitability

Prey items caught through digging, varied not only in biomass (2 g – 2 000 g) but also in handling time (digging time + eating time). The digging effort expended to catch different prey items varied according to prey species, from a shallow scrape for prey such as barking geckoes to several large holes with mounds of earth ≤ 40 cm high for scorpions, snakes and rodents. The average digging time required (minutes spent digging) for the successful capture of the ten most common prey species caught through digging was significantly different (Kruskal-Wallis; H (9, n = 1482) = 229.42, $p < 0.05$; Table 2.2). There were no significant differences when using an individual honey badger as the sampling unit (Kruskal-Wallis). The barking geckoes (1 min) and skinks (2 min) required the least effort, while the large snakes, such as mole snake (9 min) and Cape cobra (10 min) required the most effort. Within the common small mammal species, the hairy footed gerbil (3 min) required less digging effort than Brant's gerbil (4 min) and the striped mouse (8 min).

When prey profitability was estimated for the ten most common prey species as biomass consumed (g) per minute of handling time, the results showed that the large snakes (*P.cana; N. nivea*) were the most profitable prey species and were 4 - 8 times more profitable than the

Table 2.2 Estimations of the handling time (digging time + eating time) required for the successful capture of ten common food items eaten by honey badgers (5 females; 4 males) in the KTP. Prey items are presented in order of overall profitability (g / handling time).

Prey species		Handling time (min)				Profitability
		Digging			Eating	(g / min.)
		♀♀	♂♂	Overall	Overall	
Mole snake *P. cana*	(n = 23)	7.6 (1.9)	11.7 (2.8)	9.3 (1.7)	24	45
Cape cobra *N. nivea*	(n = 12)	11.8 (2.7)	6.8 (3.8)	10.1 (2.2)	12.3	31.3
Horned adder *B. caudalis*	(n = 20)	3.9 (1.7)	2.2 (0.5)	3.4 (1.2)	6.5	20.2
Brant's gerbil *T. brantsii*	(n = 145)	3.8 (0.5)	3.8 (0.6)	3.8 (0.4)	1.5	12.1
Hairy-footed gerbil *G. paeba*	(n = 327)	2.7 (0.3)	2.1 (0.2)	2.5 (0.2)	1.6	6.3
Giant ground gecko *C. angulifer*	(n = 101)	2.7 (0.3)	2.0 (0.3)	2.5 (0.2)	1.2	6.2
Barking gecko *P. garrulous*	(n = 527)	1.3 (0.1)	1.3 (0.2)	1.3 (0.04)	<1	3.8
Striped mouse *R. pumilio*	(n = 40)	9.7 (2.4)	6.3 (1.6)	7.8 (1.4)	2.2	3.2
Kalahari tree skink *M. occidentalis*	(n = 120)	2.2 (0.5)	1.9 (0.2)	2.0 (0.2)	<1	2.5
Yellow thintailed scorpion *O. wahlbergii*	(n = 167)	2.4 (0.3)	1.8 (0.4)	2.3 (0.3)	1	2.2

two common small mammals (hairy footed gerbil; Brant's gerbil), and 18 times more profitable than scorpions and tree skinks for a foraging honey badger (Table 2.2).

The largest prey species caught by a honey badger in the KTP during the study was the springhare (2 000 g). As noted above (section 2.4.1.3), one female honey badger (Af16) was observed to consistently catch springhares at night (n = 25) by following their scent, and chasing them above ground for distances up to 300 m until the springhare entered an escape burrow. The springhare was then cornered and killed in the burrow. Once a springhare had been caught, no further foraging was observed for that night. The average profitability index for springhares for the honey badger using this individualized hunting technique was calculated as: 2000 g / (14 min digging + 4 min spoor tracking) = 111 g / min handling time (n = 23). Although eating time was unknown as it occurred in a burrow, the profitability of a large prey item such as a springhare was 2.5 times that of the next most profitable item, the mole snake (45 g / min). While this female's cub was observed to use this same hunting technique successfully once independent of her mother, this was not observed in other habituated honey badgers, which ignored springhares that were above ground despite their high profitability. Other large prey items, such as the cubs and pups of felids and canids were caught by other habituated honey badgers and are likely to have similarly high profitability indexes. Since visual observations of the capture of these prey items were rare, this precluded further analysis.

2.4.2 Seasonal variation in diet

There was a clear seasonality in the diet with significant differences in the frequency of prey categories in the three seasons ($\chi^2 = 319$, $p < 0.001$, Table 2.3). Both the niche breadth and Brillouin index were highest in the hot-wet season and lowest in the hot-dry with the cold-dry season intermediate (Table 2.4). In contrast the species richness of the diet in the hot-dry

Table 2.3 Seasonal differences in the diet, expressed as percentage frequency of occurrence and percentage biomass contributed by each prey category to overall diet of honey badgers in the KTP.

	Prey consumed						
Prey category	% Frequency			Stats test[2]	% biomass		
	Cold-dry (n=1052)	Hot-dry (n=1364)	Hot-wet (n=551)		Cold-dry	Hot-dry	Hot-wet
Insects	0	0.8	1.8	$\chi^2 = 7.6$ $p < 0.05$	0	0	0.1
Solitary bee larvae[1]	6.7	0.8	0.7	$\chi^2 = 7.6$ $p < 0.05$	8.5	0.5	0.1
Scorpions	12.4	3.7	6.7	$\chi^2 = 97$ $p < 0.001$	2.6	0.2	0.3
Small reptiles (<100g)	41.0	49.6	32.7	N.S	10.8	3.6	1.1
Large reptiles (>100g)	1.4	5.4	13.8	$\chi^2 = 87$ $p < 0.001$	25.1	41.2	58.4
Small mammals (<100g)	37.6	36.2	39.3	$\chi^2 = 30.3$ $p < 0.001$	39.4	14.9	3.9
Large mammals (>100g)	0.3	2.0	3.8	$\chi^2 = 39.3$ $p < 0.001$	12.1	36.1	35.4
Birds	0.7	1.5	1	N.S	1.6	3.5	0.8

[1] = For solitary bee larvae, % frequency refers to number of feeding events not the number of individuals eaten, % biomass was estimated based on total time spent digging for larvae in each season. (section 2.3.1.2).

[2] = For chi-squared analysis, the number of prey items eaten in each season was used

Table 2.4 Seasonal differences in the diversity (Levins niche breadth index and Brillouin index) and species richness of the diet of honey badgers in the KTP.

Index of diet	Season		
	Hot-wet	Cold-dry	Hot-dry
Niche breadth	4.5	3.8	2.9
Brillouin index	0.6	0.6	0.5
Species richness	35	25	59

season was more than twice that of the cold-dry season, with the hot-wet season intermediate at 35 prey species (Table 2.4). While the consumption of small reptiles and birds showed no significant seasonal variation, there were significant seasonal differences in the consumption of all the other food categories, particularly scorpions and large reptiles (Table 2.3). Small mammals (< 100 g) and small reptiles (<100 g) were the most common prey items and together contributed greater than 70 % of the prey numbers eaten in each season and were particularly common in the hot-dry season when they made up 86 % of the diet (Table 2.3). In terms of biomass, their importance in the diet was not as consistent. The relative frequency of small mammals in the diet varied by only 3 % across the seasons, but their biomass contribution changed substantially from 39 % of the biomass consumed in the cold-dry season to only 4 % in the hot-wet season (Table 2.3). This same pattern was seen in the small reptiles, where their relative frequency of occurrence in the diet remained relatively constant across all the seasons, but their biomass contribution declined dramatically from the cold-dry season to the hot-wet season (Table 2.3).

The hot-wet season diet was characterized by the consumption of large numbers of snakes (reptiles >100 g) and because of the large size (500 –1500 g) of the most common prey snakes (mole snake *P. cana*; puff adder *B. arientans*, Cape cobra *N. nivea)*, they contributed 58 % of the biomass consumed in this season. While snakes did not disappear from the diet in the cold-dry season, they only contributed 25 % of the total biomass compared to the 39 % biomass contribution of small mammals (Table 2.3).

Large mammals were relatively rare in the diet (< 5 %), but they made an important biomass contribution and were particularly important in the warmer months of the year during the breeding season of the bat-eared fox *O. megalotis*, Cape fox *V. chama*, and African wild cat *F. lybica* (Skinner & Smithers, 1990) when the young were vulnerable to predation.

Scorpions, birds and insects did not represent more than 5 % of prey biomass in any season (Table 2.3).

2.4.3 Annual changes

When data were analyzed per season per year, there was no clear seasonal pattern in the consumption of small mammals. However, their frequency of occurrence in the diet was positively correlated with the relative abundance of small mammals in the study site estimated from rodent trapping (Figure 2.1). Both small reptile and scorpion consumption were significantly negatively correlated with the consumption of small mammals (small reptiles: $n = 8$, $r_s = -0.83$; $p < 0.01$; scorpions: $n = 8$, $r_s = -0.75$; $p < 0.05$).

No food categories showed any significant correlations between their percentage frequency in the diet and rainfall or temperature, except for the consumption of large reptiles (snakes), which is significantly positively correlated with temperature ($n = 8$, $r_s = 0.69$; $p < 0.05$). Contrary to previous years, small mammal densities were low in the cold-dry season of 1999 (Figure 2.2) and small mammals only contributed 23.4 % of the diet in frequency, while both small reptiles and scorpions were eaten in unexpectedly high numbers (Figure 2.2; Figure 2.3). Tsama melons and solitary bee larvae (Figure 2.4) both showed a sharp increase in the diet in the cold-dry season of 1998 and were noticeably abundant during this season. Solitary bee larvae were particularly unusual as they were not recorded in the diet in 1997, but were important prey items during 1998 reaching a peak (19.9 % biomass contribution) in the cold dry season of this year. They disappeared almost entirely from the diet in 1999. In 1999 individuals were seen to revisit old larvae sites but did not dig there except for one instance in

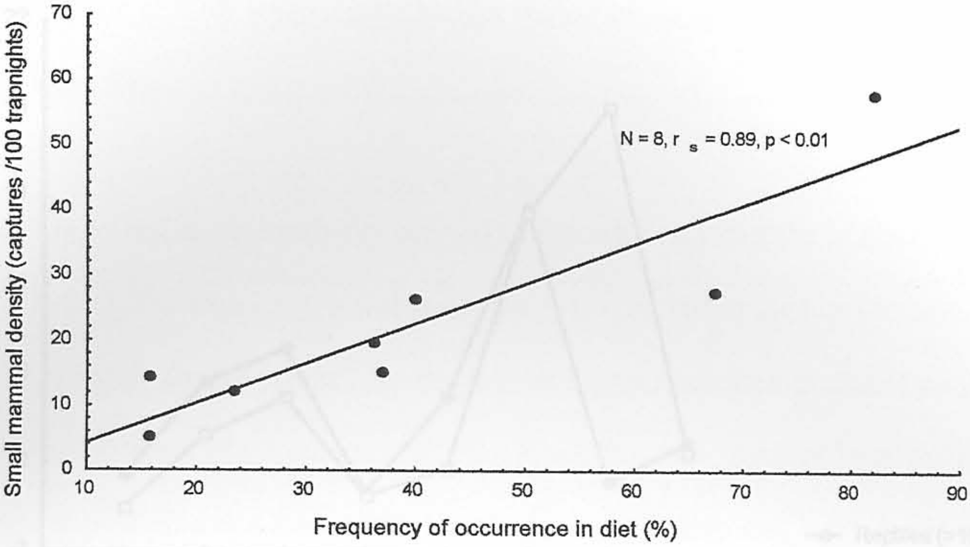

Figure 2.1 The relationship between percentage frequency of small mammals consumed by honey badgers and the relative abundance of small mammals estimated from rodent trapping from the cold-dry season 1997 to the hot-dry season 1999.

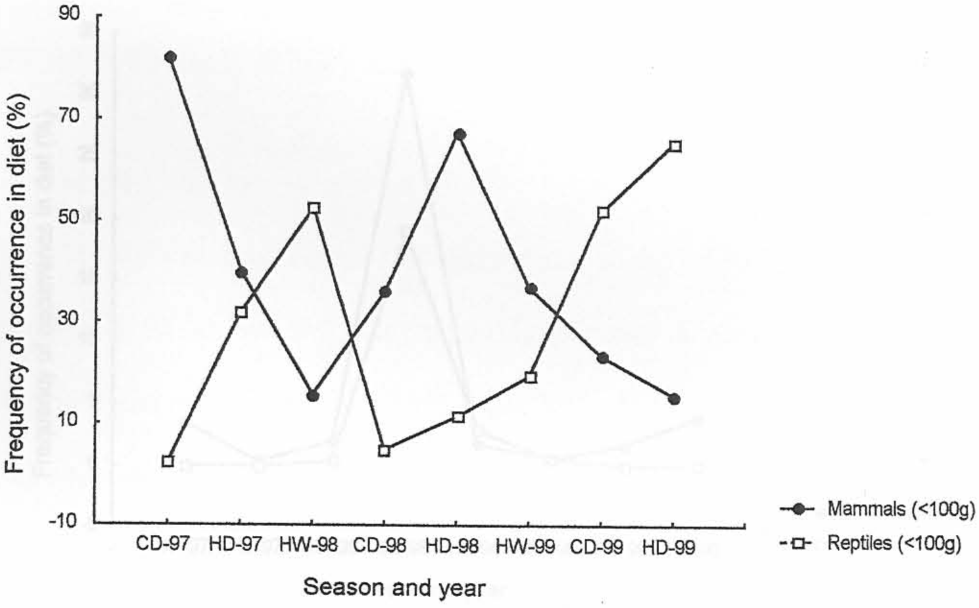

Figure 2.2 Annual and seasonal changes in the proportions of small reptiles, scorpions and small mammals in the diet of honey badgers in the KTP, from visual observations

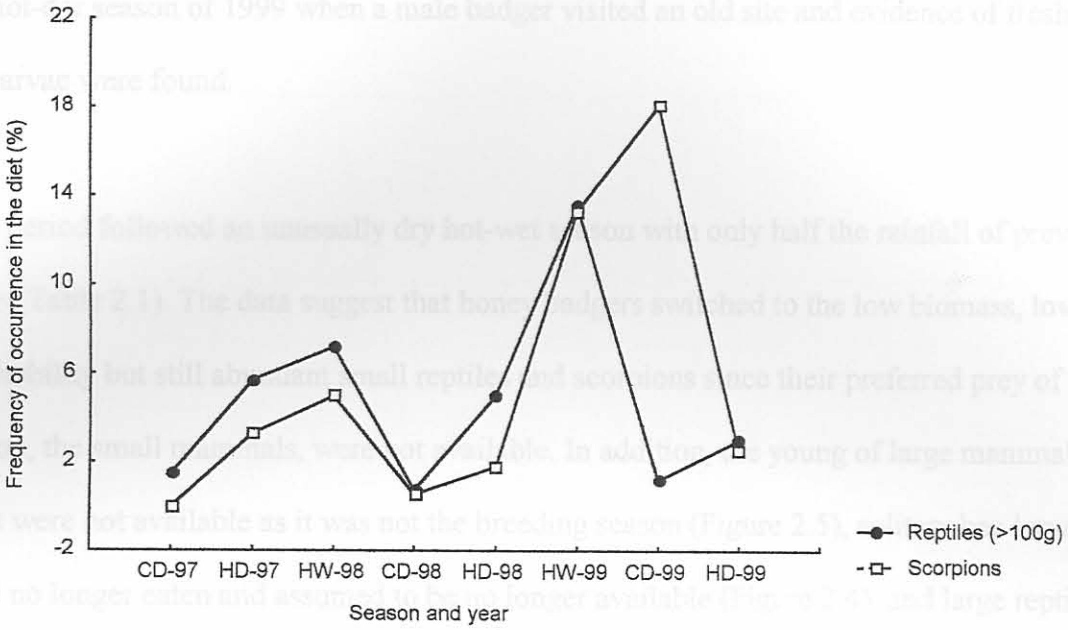

Figure 2.3 Seasonal and annual changes in the frequency of occurrence of scorpions and large reptiles in the diet of honey badgers in the KTP from visual observations.

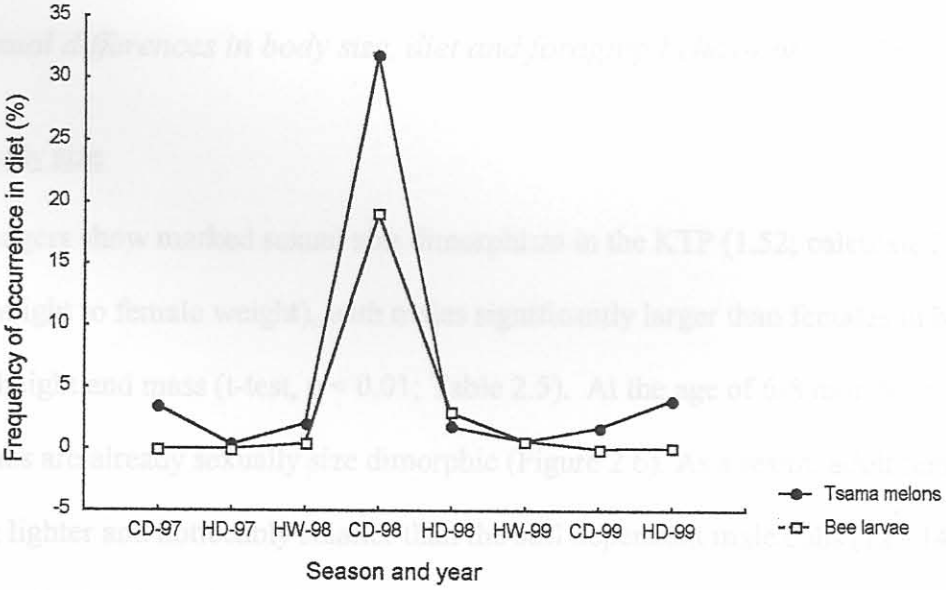

Figure 2.4 Seasonal and annual changes in the frequency of occurrence of tsama melons and solitary bee larvae in the diet of honey badgers in the KTP, showing the peak in the diet in the cold dry season of 1998 in both food categories.

the hot-dry season of 1999 when a male badger visited an old site and evidence of freshly dug out larvae were found.

This period followed an unusually dry hot-wet season with only half the rainfall of previous years (Table 2.1). The data suggest that honey badgers switched to the low biomass, low profitability but still abundant small reptiles and scorpions since their preferred prey of this season, the small mammals, were not available. In addition, the young of large mammals and birds were not available as it was not the breeding season (Figure 2.5), solitary bee larvae were no longer eaten and assumed to be no longer available (Figure 2.4), and large reptiles were inactive at this time of year. A 3-month-old honey badger cub, no longer suckling but still entirely dependent on her mother for food, starved to death during this period (confirmed by a post mortem done by Dr D. Grobler, Kruger National Park veterinarian).

2.4.4 Sexual differences in body size, diet and foraging behaviour

2.4.4.1 Body size

Honey badgers show marked sexual size dimorphism in the KTP (1.52; calculated as the ratio of male weight to female weight), with males significantly larger than females in body length, shoulder height and mass (t-test, $p < 0.01$; Table 2.5). At the age of 6-8 months male and female cubs are already sexually size dimorphic (Figure 2.6). As a result, adult females are at least 2 kg lighter and noticeably smaller than the still dependent male cubs (12 –14 months old) during the final months of dependency (Chapter 7).

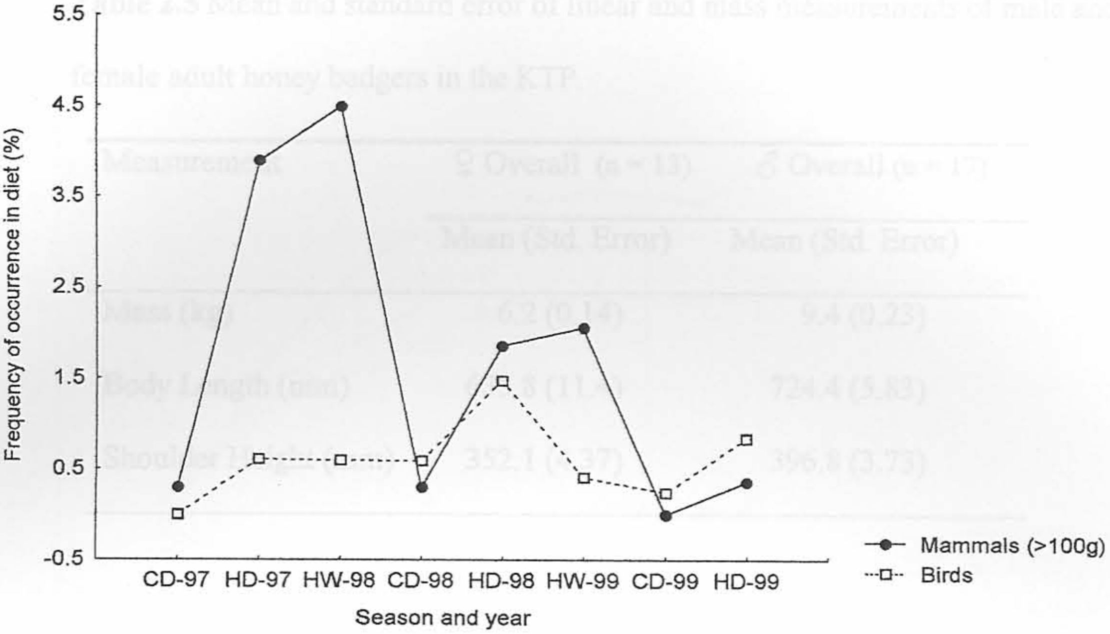

Figure 2.5 Seasonal and annual changes in the frequency of occurrence of large mammals and birds in the diet of honey badgers in the KTP.

Table 2.5 Mean and standard error of linear and mass measurements of male and female adult honey badgers in the KTP.

Measurement	♀ Overall (n = 13)	♂ Overall (n = 17)
	Mean (Std. Error)	Mean (Std. Error)
Mass (kg)	6.2 (0.14)	9.4 (0.23)
Body Length (mm)	635.8 (11.4)	724.4 (5.83)
Shoulder Height (mm)	352.1 (4.37)	396.8 (3.73)

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

2.4.4.2 Diet

Small mammals (<100 g) and small reptiles (<100 g) were the most common prey of both sexes and together contributed >75 % of the prey items in both females and males (Table 2.6). Larger reptiles (>100 g), made up exclusively of large snakes, were the largest contributors in terms of biomass (females 46.0 %; males 53 %) with larger mammals (>500 g), contributing over 30 % in female diets and 23 % in male diets, and ranked second in importance (Table 2.6).

There were no intersexual differences in the rank order of biomass consumed in the top five prey categories (Table 2.6), and overall species richness and niche breadth were similar in both sexes (Table 2.6). Seasonally, females and males also showed a similar pattern in prey diversity with the highest value for the niche breadth index in the hot-wet season (3.3 & 4.1), and similar lower values in the cold-dry (2.3 & 2.6) and hot-dry season (2.3 & 2.7). In all seasons the prey diversity was slightly higher for males than females.

Since honey badgers are sexually size dimorphic, it is possible that prey size may be a better indication of sexual differences in diet than prey type. However, there was no significant difference in the number of large (>100 g; 8.6 % vs. 7.3 %), medium (5 - 100 g; 79.4 % vs.82.3 %) or small (< 5g; 12 % vs. 9.8 %) sized prey taken by female and male badgers respectively. Neither were there any significant sexual differences in the amount of time spent digging (digging effort) for any of ten common prey species (Table 2.2).

Table 2.6 Sexual differences in the diet of habituated honey badgers (five females, four males) in the KTP expressed as the percentage frequency and percentage biomass contributed by each prey category to overall diet. The niche breadth index and species richness of male and female diets are given for comparison.

	♀ Diet (n = 1658)				♂ Diet (n = 1024)			
Prey category	% Freq.	Rank	% Biomass	Rank	% Freq.	Rank	% Biomass	Rank
Insects	0.5	7	0.06	8	0.9	8	0.06	8
Solitary bee larvae	0.1	8	0.1	7	6.3	3	3.0	6
Scorpions	10.8	3	0.6	6	3.0	5	0.1	7
Reptiles (<100 g)	48.4	1	3.4	4	37.1	2	4.2	4
Reptiles (>100 g)	6.2	4	45.7	1	4.7	4	52.6	1
Mammals (<100 g)	31.0	2	11.9	3	45.5	1	12.9	3
Mammals (>100 g)	2.2	5	36.8	2	1.0	7	22.5	2
Birds	0.8	6	1.4	5	1.5	6	3.6	5
Niche breadth	2.89				2.84			
Species richness	42				46			

2.4.5 Foraging behaviour

2.4.5.1 Hunting techniques

The honey badger is a solitary forager, and on no occasion were two adult honey badgers observed to hunt cooperatively. Its most important sense for finding food is almost certainly olfactory. Individuals were often seen to stop, smell with their heads turned up wind and then change their foraging direction towards a food item. Overall two types of movements were identified, the slow winding walk with frequent investigation of scent trails and prey burrows utilized by both sexes when intensively foraging and the faster, directional jog- trot used only by males engaged in social activities (patrolling of latrines, scent marking and searching for females; Chapter 7). Whilst engaged in these social activities, males caught 9.8 % of their prey biomass opportunistically.

There were no significant intersexual differences in the method of prey capture and both sexes caught the majority (females: 85 %; males: 80 %) of their prey by digging, with similar percentages of prey caught above ground (females: 12 %; males: 11 %). Female honey badgers did catch slightly less prey through climbing and ripping off bark (3 % vs. 9 %) than males.

When digging for gerbils with extensive burrow systems and numerous escape holes (e.g. *G. paeba* and *T. brantsii*), honey badgers purposefully closed potential escape holes with their front paws and then dug alternatively at two or three holes, chasing the rodent from one end of the tunnel to the other by their digging activities. By moving of the tail and "paddling" the hind feet in one hole, while waiting motionless at the edge of another hole, rodents were chased towards the forepaws for capture.

Adult honey badgers are also accomplished climbers and are able to raid raptor nests and bee hives and remove the bark from trees in search of lizards and skinks. Snakes were caught above ground by following scent trails and through digging. In the KTP, only 0.5 % of all prey items eaten were scavenged, and on no occasion were honey badgers seen to scavenge from the carcasses of prey killed by the larger carnivores. In addition, there was no evidence in the KTP to suggest that the honey badger castrates larger prey items (Stevenson-Hamilton, 1947).

2.4.5.2 Rate of food intake, digging success, time spent foraging

Honey badgers foraged every day even when the previous day's foraging had been successful. On average male honey badgers consumed more food per day than females, although this was not a significant difference (Table 2.7). There was no significant difference in the mean percentage of their body weight consumed per day (Table 2.7), although it varied widely. On one occasion a male badger (HB12), weighing 11 kg, consumed at least 6.6 kg of meat in one day, comprising four adult mole snakes, two adders and seven mice. The previous day the same male had eaten 2.6 kg, and the following day he ate 3.3 kg and caught an additional two Cape cobras which he killed but abandoned above ground before going into a burrow to rest. To remove the possibly confounding effects of badgers of different ages and weights within a sample, two adult middle-aged honey badgers, one male (Am12) and one female (Am38), of known body weight were directly compared. The home range of the female lay within the home range of the male, and they utilized similar habitat over a similar time period (1998/1999). The same result was obtained, with both the male and the female ingesting 0.1 kg of food / kg of body mass/ day (Table 2.7).

Table 2.7 The average daily consumption of male and female honey badgers determined from continuous 24 hour observation periods and expressed as the mean (standard error) biomass of food eaten per day and the biomass ingested per kilogram of body weight per day with a direct comparison between one male and one female honey badger of known body mass.

Sex	Mass (kg)	Consumption (kg / day)	Consumption (kg / kg bodyweight /day)
♂ Overall (n = 64)	9.4 (0.94)	1.3 (1.2)	0.1 (0.15)
♀ Overall (n = 67)	6.2 (0.52)	0.9 (0.89)	0.2 (0.17)
♂-HB12 (n = 31)	11	1.0 (0.46)	0.1
♀-HB38 (n = 44)	6	0.7 (0.26)	0.1

While males and females without cubs consumed all the food that was caught (i.e. foraging rate = consumption rate; Table 2.8), this was not true for females provisioning dependent cubs. A single cub was raised at a time with an extended dependency of 12 -14 months (Chapter 7) during which time the cub was almost entirely dependent on the adult female for food after weaning at 2 - 3 months. When cubs were 3 - 6 months old, they were fed an average 23 % (S.E = 6.6; n = 16 observation periods) of the food biomass caught by a female during a foraging period, and this increased to 45 % (S.E. = 2.7; n = 66 observation periods) from six months until independence. The consumption rate of females tended to decrease when they had dependent cubs compared to when they foraged alone, while the foraging rate tended to increase, although these differences were not significant (Table 2.8). Overall females, both with and without cubs, had a significantly higher consumption rate and foraging rate than males (Table 2.8).

Seasonally, there were no significant differences in the biomass ingested per kilogram of body weight in either males or females. However, both males and females showed a similar pattern of significantly lower consumption rates in the cold-dry season compared to the hot-wet season with the hot-dry season intermediate (Table 2.9). In addition, female honey badgers showed significantly higher digging success in the cold-dry season, with the same trend in the males (Table 2.9).

Table 2.8 Comparison of consumption rate, foraging rate and digging success of male and female honey badgers in the KTP. Within each category the differences were not statistically significant when using individual honey badgers (five females; four males) as the sampling unit. Sample size (n) represents the number of observation periods used for the analysis in each category.

Hunting behaviour	Females		Males	Significance test
	♀ no cubs $\bar{x}$ (SE; n)	♀ dependent cubs $\bar{x}$ (SE; n)	♂ overall $\bar{x}$ (SE; n)	
Consumption rate (g eaten / foraging min.	4.9 (1.0; 45)	3.4 (0.5; 76)	2.6 (0.4; 167)	Kruskal-Wallis $H = 18.3$; $p < 0.05$
Foraging rate (g caught / foraging min).	4.9 (1.0; 45)	5.9 (0.8; 76)	2.6 (0.4; 167)	Kruskal-Wallis $H = 21.9$; $p<0.05$
Digging success[12] (%)	40 (2.1; 45)	41.6 (2.6; 76)	49 (2.2; 167)	ANOVA Not sign

[1] = Proportions were arcsine transformed to normalize for ANOVA analysis, then backtransformed for means (Zar, 1999)

[2] = Digging success was calculated as the percentage of digging events that had a successful outcome (prey was caught) per observation period. A digging event consisted of 1-6 holes dug for a single prey item.

Table 2.9 Seasonal variations in consumption rate, hunting success and biomass ingested per gram of body weight of honey badgers in the KTP.

Foraging behaviour	Females $\bar{x}$ (S.E.; n)				Males $\bar{x}$ (S.E.; n)			
	Hot-wet	Cold-dry	Hot-dry	Significance test	Hot-wet	Cold-dry	Hot-dry	Significance Test
Consumption rate (g / min)	4.7 (0.8; 55)	1.1 (0.3; 39)	3.7 (0.5; 82)	Kruskal-Wallis $H = 13.4$ $p < 0.05$	5.7 (1.1; 26)	1.3 (0.3; 71)	3.5 (0.6; 70)	Kruskal-wallis $H = 13.63$ $p < 0.05$
Digging success^{1+2}	32.3 (2.4; 55)	41.7 (1.9; 39)	37.8 (3.6.9; 82).	ANOVA $F = 4.85$ $p < 0.05$	36.0 (3.9; 26)	39.7 (1.9; 71)	39.1 (1.7; 70)	Not sign.
Grams ingested / kg of body mass/day	0.2 (0.03; 24)	0.1 (0.05; 10)	0.1 (0.02; 33)	Not Sign	0.1 (0.03; 10)	0.1 (0.02; 24)	0.2 (0.03; 27)	Not sign

[1] = Proportions were arcsine transformed to normalize for ANOVA analysis, back transformed to calculate means (Zar, 1999).

[2] = Digging success was calculated as the percentage of digging events that had a successful outcome (prey was caught) per observation period. A digging event consisted of 1-6 holes dug for a single prey item.

2.5 Discussion

While the honey badger is frequently reported to be omnivorous including a wide variety of wild fruits, bulbs and tubers in its diet (Fitzsimons, 1919; Dragesco-Joffe, 1993), it was almost exclusively carnivorous in this study. Tsama melons were the only vegetable matter eaten, and these appeared to be eaten primarily for their moisture content. This is in sharp contrast to the European badger, which eats a wide variety of plant (cereal and fruit) and animal material (Neal & Cheeseman, 1996) but similar to the primarily carnivorous diet of the American badger *Taxidea taxus* (Messick & Hornocker, 1981; Neal & Cheeseman, 1996).

Optimal foraging theory states that a predator chooses prey types based on a trade-off between costs and benefits that will give the maximum net benefit to the individual. The profitability of prey items may change over time as a decrease in prey biomass will increase the foraging costs of the preferred prey through increased search time (Krebs & Davies, 1987). In support of the prediction of prey switching, the data show that the honey badger is a generalist and opportunist with seasonal shifts in diet that appear to reflect changes in food availability. Similar seasonal shifts in diet have been documented in a variety of north temperate mustelid species (Dunstone, 1993; Lode, 1994; Zielinski *et al.*, 1983; Genovesi *et al.*, 1996; Martinoli *et al.*, 2001). Small mammals are the honey badger's staple prey, and the clear correlation between the abundance of small mammals in the diet and small mammal density suggests that when small mammals are less abundant they are less frequently eaten and the honey badger shifts to other less profitable prey items, particularly small reptiles and scorpions. The "switch" to consuming the less profitable prey items did not appear to be related to a change in the abundance of the less profitable prey, but rather to a decrease in the abundance of the preferred prey (small mammals) and an associated increase in search costs.

Both larger mammals and birds are eaten in greater numbers during the warmer months than in the cold dry season, and this can be explained by the increase in availability of young canids, felids and raptors during their respective breeding seasons (Skinner & Smithers, 1990; Steyn, 1982). While no data were collected on the variation in actual abundance of other prey categories during this study, small reptile populations appear to be highest in late summer (hot-wet season; W. Haacke, *in litt*, 2001.), while scorpions (L. Prendini, pers. comm.) and large reptiles (B. Branch, *in litt*. 2001) are unlikely to vary in their actual abundance in the short term (monthly) due to their long life spans and slow population turnover. It has, however, been speculated that prey may be easier to detect when active (Zielinski, 1988; Samson & Raymond, 1995). For an opportunistic predator such as the honey badger, which locates its prey through scent trails, strong seasonal activity patterns of prey may substantially influence a honey badger's perception of their abundance and availability.

All scorpion species in the KTP are only active in the warmer months of the year with little movement in the cold-dry season (L. Prendini, pers. comm.), and snakes and small reptiles show a similar pattern of decreased activity with a general dormancy in winter that reflects the cold temperatures (B. Branch, *in litt*, 2001). During the hot-dry season there is increased snake and small reptile activity due to the return of warmer weather and a consequent increase in prey availability. During periods of low prey activity, a honey badger's encounter rate of that prey is likely to be reduced (increased search time) and other more abundant prey should be of increased importance (Ben-David *et al.*, 1997). The tendency for the honey badger to eat more large reptiles in the warmer months than in the cold dry season in all years of the study and the clear correlation between snake consumption and temperature, suggests this is indeed the case.

In the cold-dry season only 25 of the 66 prey species that are known to be prey of the honey badger in the KTP are eaten and the consumption rate is four times lower than in the hot-wet season. Since the foraging rates of females with dependent cubs show a similar decline from 5.2 g / min in the hot wet season to only 1.4 g / min in the cold dry season it is likely that cubs also obtain proportionally less food during these months. The starvation of a cub in the cold dry season of 1999, when small mammal densities were particularly low and honey badgers were primarily eating low biomass, low profitability small reptiles and scorpions, suggests that small mammal densities may be critical in this season, particularly for females with the high energetic costs of reproduction and cub rearing.

The hot-dry and hot-wet season appear to be the time of food abundance for both male and female honey badgers in the KTP, with a wide variety of food species available and high consumption rates (grams per foraging minute) compared to the cold-dry season. The increased number of prey species available in the hot-dry season is reflected in the high species richness, while the preference for species with a relative high profitability (i.e. snakes) results in lower dietary diversity and niche breadth. Conversely, while fewer species are eaten in the cold-dry season, food is more evenly distributed across all the food categories. This agrees with the optimal foraging hypothesis (Perry & Pianka, 1997), which suggests a generalist feeder will increase dietary diversity in response to a decrease in prey availability. However, in the hot-wet season the diet of the honey badger is characterized by high consumption rates, high species richness and high dietary diversity. These data suggest that dietary diversity may also increase during times of high prey availability when a large variety of profitable prey species are available.

Surprisingly, despite the decreased consumption rate in the cold dry season, the daily biomass ingested per kg of body weight did not differ significantly between the seasons in either sex. Gittleman and Thompson (1988) suggest that behavioural compensation is potentially the most important tactic for meeting additional energy requirements, particularly the demands of reproduction. Analysis of the time budgets of honey badgers as part of this study, shows that honey badgers appear to compensate for the decrease in consumption rate in the cold-dry season by increasing the amount of time spent foraging per day to almost double that of the hot-wet season (Chapter 3). Unfortunately no data are available on seasonal changes in body weight.

The overall patterns of seasonal and yearly changes in diet are further complicated by sexual and individual differences in diet and foraging behaviour. Our results confirm that in common with many other members of the family Mustelidae, the honey badger is sexually size dimorphic with males a third larger than females. Moors (1980) compared dimorphism in 14 species of mustelids (excluding the honey badger) and values ranged from 1.15 (the European badger) to 2.24 (weasel), with extreme dimorphism defined as a value greater than 1.6 (Ralls, 1977). The value calculated for the honey badger in this study (1.52) is defined as moderate dimorphism and is similar to the average level of dimorphism recorded for the family as a whole (1.58). Within the medium-sized mustelids, the honey badger has similar dimorphism levels to the wolverine *Gulo gulo* (Moors, 1980) and the Eurasian otter *Lutra lutra* (Kruuk, 1995) but is substantially more dimorphic than the European badger *M. meles* (1.15; Moors, 1980) and the North American badger *Taxidea taxus* (1.2; Messick & Hornocker, 1981).

In support of the hypothesis that sexual size dimorphism reduced intersexual resource competition, preliminary data collected in the KTP by Kruuk & Mills (1983) suggested that male and female honey badgers utilize different foraging strategies, with females "short distance foragers" covering an average of 5 km per day, catching predominantly small prey, while males are "long distance foragers" covering an average distance of 27 km per day and catching larger prey items. Results from this study do not clearly support this view, since both sexes are "short distance foragers" when intensively foraging. While long distance walking is exclusively recorded in male honey badgers (Chapter 5), less than 10 % of their overall intake is caught when engaged in this behaviour. Instead, long distance walking is more closely associated with the social activities of males (i.e. latrine checking, searching for females; Chapter 7) than hunting behaviour, although some prey is caught opportunistically.

While there is an intersexual difference in the frequency of species taken in each prey category, there is no difference in the ranking of prey categories, with reptiles (>100 g) and large (>100 g) and small (<100 g) mammals the top three ranking prey categories in terms of biomass, in both sexes, in the same order. These significant differences in frequency may be due to individual differences in diet (Kruuk, 1995) e.g. the female that specialized in springhares, or to differences in food availability in different seasons and years, which are exaggerated by the small sample size of habituated badgers. Alternatively these differences might be a consequence of sexual differences in the spatial organization of honey badgers (Chapter 5), as adult males (548 km^2) forage over much larger areas than females (139 km^2). The prey categories eaten less frequently by females i.e. small mammals, solitary bee larvae, and birds fluctuate widely in abundance and, in the case of solitary bee larvae and breeding birds, appear patchily distributed. It is possible that since females forage intensively over the same ground daily (Chapter 5), their encounter rates of patchy prey items are reduced in times of low abundance due to prior exploitation or reduced distribution. They might then utilize greater numbers of seasonally more stable and abundant prey such as small reptiles and scorpions, although these are less profitable (Ben-David *et al.*, 1997). Conversely, males forage over extensive areas and their encounter rate of more patchy prey items is less likely to be affected by prior exploitation or reduced distribution.

In contrast to data from other mustelids that show sexual size dimorphism (Erlinge, 1981; Moors, 1980), there is no evidence that the smaller female honey badgers take smaller prey than males. Both sexes kill prey ranging in size from insect larvae (1 g) to springhares (2000 g). In addition, there are no sexual differences in digging success or in the digging effort required to catch any of ten common prey species of varying size. There is therefore no evidence to suggest that differently sized sexes are more or less efficient at catching the same prey or that males and females utilize different foraging strategies.

The data show that males consume more prey per day than females, and this is expected given that basal metabolic rate is proportional to body mass$^{0.73}$ (McNab, 1963) and males are larger than females. To meet their energetic demands, males forage for 5 – 6 % longer than females each day (Chapter 3) and catch food opportunistically during social activities and this counters their low consumption rate. Although females are expected to have higher energetic demands due to pregnancy, lactation and cub rearing (Oftedal & Gittleman, 1989) there is no significant difference in the daily food intake per unit of body weight in males and females. It is possible that while reproduction and cub rearing are energetically costly for female honey badgers, so to are social activities such as scent marking and long distance walking in males (Chapter 3). As a result the energetic demands per unit of body weight are similar for both sexes. Overall the daily food intake per unit of body weight is similar to the value of 15 % found for otters (Kruuk, 1995).

It is evident that while male and female honey badgers show a significant difference in body size, they show few differences in diet and foraging behaviour and no differences that can be directly attributed to sexual size dimorphism. These results, therefore, do not support the hypothesis that size dimorphism is primarily an adaptation to reduce intersexual competition for food (although this might only become evident during times of food stress). It could however, be that in the KTP the degree of dimorphism is not large enough to impose different nutritional requirements on each sex. Studies on the foraging behaviour, diet and the level of dimorphism in other habitats will help to elucidate this further. Sexual size dimorphism in the honey badger may be better explained by their breeding system and sexual selection (Chapter 7), rather than bioenergetics (Lups & Roper, 1988).

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- Chapter 3 -

Sexual and seasonal variation in the time budget and activity patterns of the honey badger *Mellivora capensis* in an arid environment.

3.1 Abstract

Sexual and seasonal variation in the daily time budgets and activity patterns of nine habituated honey badgers were investigated for three and half years, in the southern Kalahari. On average both sexes spend at least 50 % of the day inactive. In all seasons males spend more time engaged in social activities than females (15 % vs. 2 % overall), but there are few differences in the time spent foraging. Both sexes spend significantly more time foraging in the cold-dry season compared to the hot-dry and hot-wet seasons, and this appears to be a behavioural response to low prey availability. The daily activity schedules of both sexes show two peaks of activity. The timing of the two active periods show a strong seasonal shift from predominantly nocturnal activity in the hot-wet and hot-dry seasons to more diurnal activity (44.3 %) in the cold dry season. The honey badger appears to maximize foraging benefit on a daily level by "switching" between alternative prey species during a day according to differing prey vulnerabilities. However, it is considered unlikely that the seasonal shift in activity schedules is primarily due to a seasonal shift in prey activity since a wide variety of prey with differing activity schedules are eaten. Instead, temperature appears to be the major factor affecting seasonal activity schedules, with extreme temperatures avoided by behavioural thermoregulation i.e. by moving into a burrow.

3.2 Introduction

The proportion of time that an individual allocates to each of its activities frequently provides a good indication of its energetic priorities (Hemingway, 1999; Bekoff & Wells, 1981; Kemp & Begg, 2001). For all animals the time available for foraging is critical, as sufficient time must be allocated to meet the energetic demands of growth, maintenance and reproduction, but time must also be allocated to activities such as mating, defense of resources, predator defense and self maintenance (Bekoff & Wells, 1981; Armitage *et al.*, 1996).

The honey badger *Mellivora capensis* is a medium sized generalist carnivore that has not been well studied, and no information is available on its time budgets or activity schedules. It has recently been shown that the honey badger is sexually size dimorphic with males at least a third larger than females (Chapter 2), and it has a polygynous or promiscuous mating system. For females, the limiting resource is generally considered to be food, while in males, the limiting resource is receptive females (Sandell, 1989). It is, therefore, expected that males and females will partition their time differently as fundamental differences in male and female reproductive biology and parental investment will result in differences in energetics (Gittleman & Thompson, 1988; Hemingway, 1999). On a seasonal level, behavioural tactics of modulating activity levels and varying the amount of time spent on different behaviours provides mammals with a means of coping with a changing environment (Gittleman & Thompson, 1988; Hemingway, 1999).

By varying the timing of the active periods, animals might also affect the costs and benefits of a particular activity. Pyke *et al.* (1977) suggest that if foraging costs change as a function of the timing of the activity, the predators should distribute their activity patterns to maximize net foraging benefit. While the honey badger is generally considered to be nocturnal, diurnal activity has been observed particularly in wilderness areas, and Skinner & Smithers (1990) suggest that the honey badger may adjust its activity patterns to support its requirements and that it is only completely nocturnal in areas where it is disturbed by man. The actual timing of activity periods may be related to many factors including light /dark cycles, competition, predators, prey activity, and temperature (Bekoff & Wells, 1981; Zielinski *et al.*, 1983; Cavallini, 1993; Clevenger, 1993; Samson & Raymond, 1995). The food of carnivores often exhibits a daily cycle of activity (i.e. prey can be nocturnal, diurnal, or crespuscular), and there may be differing energetic costs associated with locating and capturing, active and inactive prey (Zielinski, 1986; 1988). As a result, Zielinski (1986) suggests that a carnivore that can anticipate a circadian peak in prey availability will be more successful at acquiring food than a carnivore that forages at random. Certainly, a variety of predators do appear to synchronize their foraging activities with the active phase of their primary prey i.e. American marten *Martes martes*; Zielinski *et al.*, 1983; Clevenger, 1993; American kestrel *Falco tinnunculus*: Rijnsdorp *et al.*, 1981; Village, 1990; Ethiopian wolf *Canis simensis*: Sillero-zubiri & Gotelli, 1995; pangolin *Manis temminckii:* Swart *et al.*, 1999). Yet in other studies, the activity schedules of carnivores are known to be primarily affected by temperature with individuals limiting above ground activity during extreme temperatures, particularly extreme cold (Bekoff & Wells, 1981; Dobson & Davis, 1986; Dunstone, 1993).

The aim of this chapter is to describe the time budget and activity patterns of free-living honey badgers in a wilderness area. In particular, the way in which male and female honey badgers partition their time between different activities in different seasons and the relationship between activity patterns, daylight, temperature and prey activity schedules are investigated.

3.3 Methods

3.3.1 Study area

The project 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 and neighbouring Gemsbok National Park, Botswana.

It is a semi desert region and is described by Acocks (1988) as the western form of Kalahari Thornveld with a very open savanna of *Acacia haemotoxylon*, *Acacia erioloba* and desert grasses. This study was primarily conducted in the central dune area of the KGNP, which is characterized by medium to high dunes on reddish sands where *A. haemotoxylon* appears in a shrublike form with occasional *Boscia albitrunca* and *A. erioloba* trees. Dune areas are interspersed with slightly undulating open plains areas, with similar plant composition but with no *B. albitrunca* trees, and pans with yellowish sands, which support shrub veld of *Rhigozum tricophorum* and *Monechma sp* (Van Rooyen *et al.*, 1984).

3.3.2 Climate

The study area falls between the 200 mm and 250 mm rainfall isohyets and is characterized by low, irregular annual rainfall (Mills & Retief, 1984). The variability of the rainfall plays a major role in the vegetation of the KTP (Leistner, 1967) and large differences in floristic composition, basal cover and density can be expected in the short and medium term (Van Rooyen, 1984). Three seasons are distinguished: the hot-wet season (HW) from January to April when the mean monthly temperature is approximately 20°C or higher and when 70 % of the rain falls; the cold-dry season (CD) from May to August when the mean monthly temperature is below 20°C and rainfall is rare and the hot-dry season (HD) from September to December when the monthly temperature is approximately 20°C and usually not more than 20 % of the rain falls (Mills & Retief, 1984). Summer maximum temperatures are 30 - 40°C, and Leistner (1967) states that when the air temperature is approximately 40°C, the sand surface can reach 70°C. In contrast, the winters are fairly severe and minimum temperatures are normally –5°C to 5°C and ground frost is common (Mills, 1977; Mills & Retief, 1984).

The weather bureau of South Africa provided daily minimum and maximum temperatures from the KGNP for the period of the study. As the study site lay within the central dune area equidistant from all collection sites, a mean seasonal temperature was calculated using the data from all three camps (Figure 3.1). Data from the nearest town, Upington (300 km NNE) were used to provide an estimate of hourly changes in temperature (Figure 3.2) as no data were available for hourly temperature changes within the KTP. The average time of sunset and sunrise for each month was calculated for a central location within the study area (Bitterpan) using a Global Positioning System (GPS).

3.3.3 Study population

Detailed capture, marking and habituation techniques are presented in Appendix A. Over 2000 hours were spent habituating nine radio-marked adult badgers (five females with five cubs and four males) to the vehicle, until they could be followed without any obvious influence on their foraging behaviour (Appendix A). Habituation also enabled us to collect information on non-habituated badgers (termed "other females" and "other males" in Appendix B) as the non-habituated individuals frequently appeared to take their cue from the habituated badgers and relaxed in our presence.

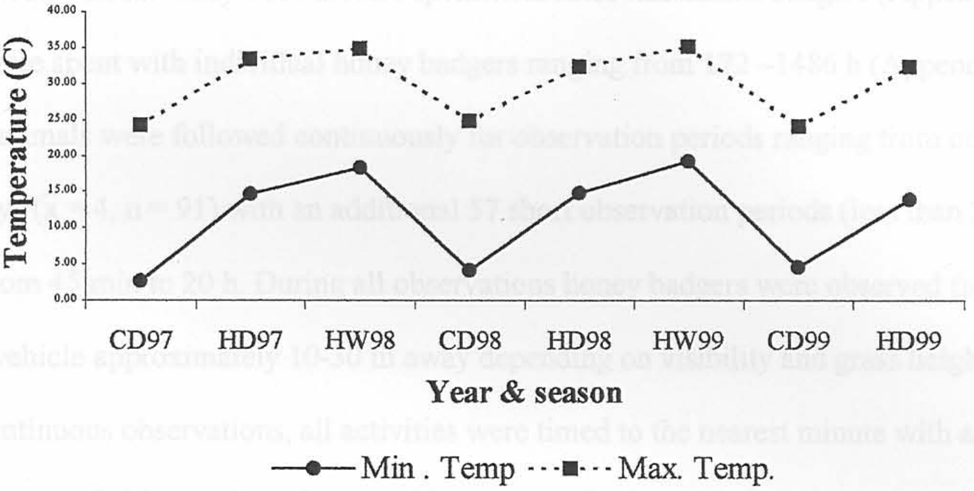


Figure 3.1 Seasonal changes in the average maximum and minimum temperatures during the study period in the KTP.

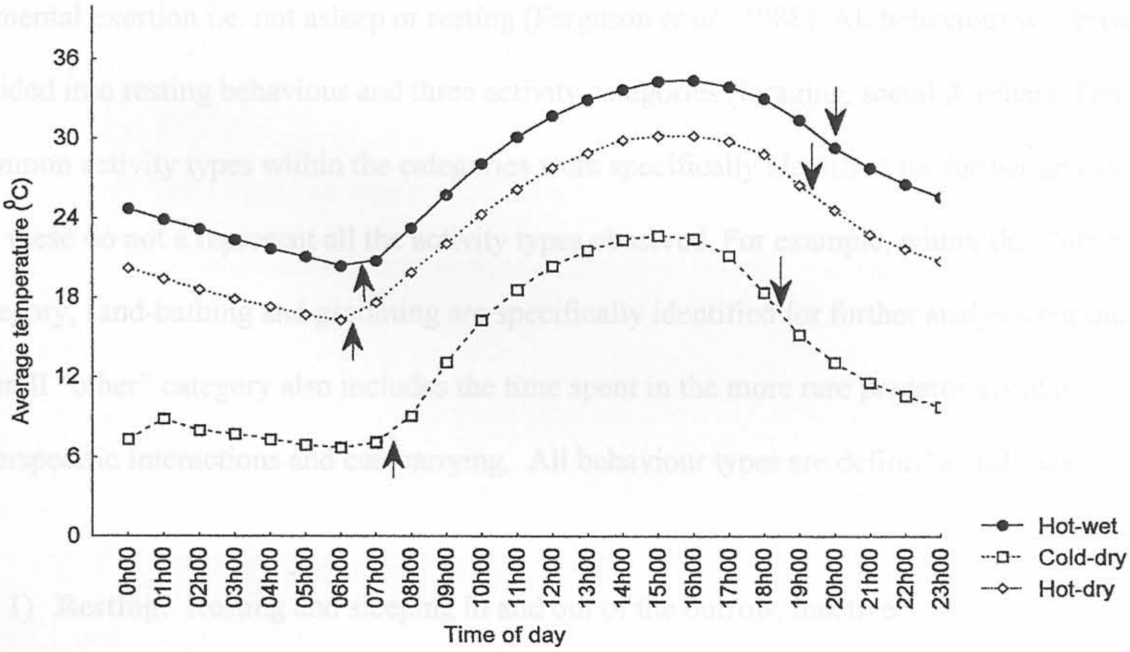


Figure 3.2 Average hourly changes in temperature in the hot-wet, cold-dry and hot-dry season calculated from the nearest town, Upington (provided by the South African Weather Bureau). The arrows indicate the average time of sunrise and sunset for each season calculated from a GPS location in the centre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

Over the course of the study 5811 h were spent with these habituated badgers (Appendix B), with the time spent with individual honey badgers ranging from 172 –1486 h (Appendix B). Selected animals were followed continuously for observation periods ranging from one to twelve days ($\bar{x} = 4$, n = 91) with an additional 57 short observation periods (less than 24 h) ranging from 45 min to 20 h. During all observations honey badgers were observed from the roof of a vehicle approximately 10-30 m away depending on visibility and grass height. During continuous observations, all activities were timed to the nearest minute with a stopwatch, recorded into a dictaphone and later transcribed onto data sheets.

3.3.4 Definition of terms

An individual was considered to be active when it was engaged in actions requiring physical or mental exertion i.e. not asleep or resting (Ferguson *et al.*, 1988). All behaviour was broadly divided into resting behaviour and three activity categories (foraging, social & other). Ten common activity types within the categories were specifically identified for further analysis, but these do not a represent all the activity types observed. For example, within the "other" category, sand-bathing and grooming are specifically identified for further analysis but the overall "other" category also includes the time spent in the more rare predator avoidance, interspecific interactions and cub carrying. All behaviour types are defined as follows:

1) **Resting:** Resting and sleeping in and out of the burrow, inactive
    a) *In hole resting*: Out of sight in a burrow for > 30 min with no sound of movement, digging or vocalizations.
    b) *Above ground resting*: Lying curled up on its side above ground with its eyes close. Frequently under a bush during the day or in a shallow hollow in the sand at night.

2) **Foraging:** Searching, climbing, digging, handling and eating prey
    - a) *Searching:* Actively looking for prey through a winding walk with frequent investigation of holes and scent trails.
    - b) *Digging:* Active hunting of a specific prey item through digging. This includes the time spent running between alternative digging holes.
    - c) *Eating & Handling:* Obviously chewing or ingesting a food item, or actively engaged in subduing a prey item.
3) **Social activities:** Intraspecific interactions, travelling / patrolling, scent marking, and cub carrying, playing
    - a) *Scent marking:* Specific behaviour associated with depositing scent marks on objects in the environment. This includes latrine visits, defecation, urination, squat marking and anal dragging (Chapter 6).
    - b) *Intraspecific interactions:* Any behaviour where two or more adult honey badgers responded to each other's actions directly. This included male-male and male-female interactions (Chapter 7) but does not include mother-cub interactions.
    - c) *Travel:* Straight line trotting with little attempt to investigate potential prey holes or items. This behaviour was directly associated with patrolling latrines and searching for conspecifics (Chapter 5).
4) **Other activities:** Sand-bathing, grooming, predator avoidance, interspecific interactions.
    - a) *Sand bathing:* Honey badger would throw sand onto its flanks and body with its front paws, while lying down.
    - b) *Grooming/scratching*: Specific periods of concentrated scratching and nibbling of the skin. Single scratching events of < 1 minute that occurred while engaged in other activities were not included.

3.3.4 Data analysis

For analysis of time budgets and active periods only data from continuous 24 h observation periods were used, with the time spent engaged in each activity (min) represented as a proportion of the total time available in a day (1440 min). These proportions were arcsine transformed to achieve normality (Zar, 1999) and analyzed with parametric statistical tests (two sample, two sided t-tests & ANOVA: Stasoft, 2000). The means were then back transformed for presentation (Zar, 1999). Preliminary tests showed no significant individual differences (5 % level) in time budgets within a particular season and sex. Data from different individuals were therefore pooled for further analysis.

To calculate the average time of day that honey badgers began and ended active periods, time units were converted to angular direction (A in degrees). For example given a time of day 06h15, $A = (360^{\circ} \times 6.25 \text{ hr}) / 24 \text{ hr} = 93.75^{\circ}$ (Zar, 1999).

The mean angle was calculated as the angle with $\cos \bar{A} = X / r$ and $\sin \bar{A} = Y / r$ where: $X = \sum_{i=1}^{n} \cos A_i / n$ and $Y = \sum_{i=1}^{n} \sin A_i / n$ (Zar, 1999). The mean time corresponding to the mean angle was then back transformed.

To standardize for the number of hours honey badgers were visually observed, activity schedules were calculated as the mean percentage of total observation time that individual honey badgers were active for each hour of the day and should be read as "relative activity". Appendix D shows the overall amount of time spent observing habituated badgers for each hour of the day in each season. The average time of sunset and sunrise for each season was calculated from a GPS location in the centre of the study area and activities were denoted as nocturnal and diurnal relative to these times.

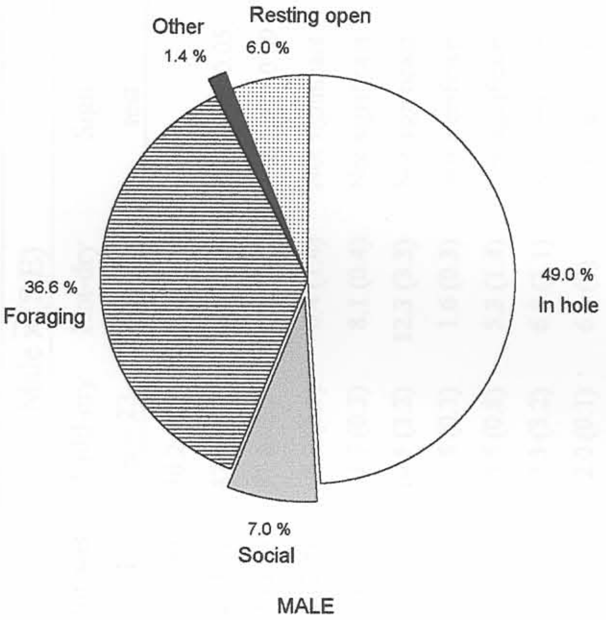
3.4 Results

3.4.1. Time budgets

3.4.1.1 Sexual differences

Overall male honey badgers were active above ground for an average 11 h of every day (45 %), and 80 % of this active time (8.5 h) was spent foraging intensively (Figure 3.3). The remainder of the above ground activity was divided between social activities (15.6 %) including intraspecific interactions, scent marking and the patrolling of latrines and "other" activities (4.4 % of the day) such as sand bathing and grooming. In comparison, females were active for only eight hours (32.9 %) a day but spent 98 % of this time foraging intensively with only 2.3 % of their active time engaged in social and other activities (Figure 3.3). There was no significant difference in the percentage of the day spent foraging in females with or without cubs (without cubs: 26.9 %; n = 37 vs. with cubs: 29.9 %; n = 27).

In all seasons males spent significantly more time engaged in social activities than females (Table 3.1; Table 3.2), although in both sexes social interactions were relatively rare and individuals were usually solitary. In particular, females were not observed to travel (long distance walking) to visit latrines and also spent less time interacting with conspecifics. While males were observed to interact directly with other males as well as females (2.2 – 7.3 % of the day; Table 3.1), females were never observed to interact with other females and were relatively rarely observed with other males (1.9 – 3.6 % of the day; Table 3.1). Females were only observed to interact with male honey badgers on four (6.3 %) of the 63 days of 24 h observation, while intraspecific interactions were observed in males on 20 days (32.8; n = 61).



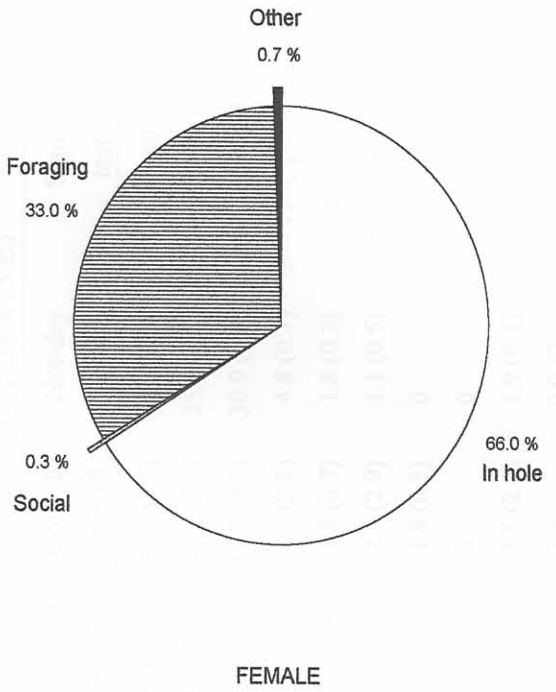


Figure 3.3 Overall sexual differences in the daily time budgets of the honey badger calculated from continuous 24 h observations of habituated individuals (Males: n = 61 days; females: n = 63 days). Social behaviour refers to latrine checking, scent marking, and intraspecific interactions while "other" refers to sand bathing, scratching, playing and short duration resting (< 30 min).

Table 3.1 A seasonal and sexual comparison of the percentage of the day the honey badger spends active, resting, foraging and engaged in social interactions and other activities. Percentages were calculated from whole day continuous observations only (five females; four males).

Behaviour		Percentage of day spent in each activity							
		Female $\bar{x}$ (S.E)				Male $\bar{x}$ (S.E)			
Category	Type	Hot-wet n = 22	Cold-dry n = 10	Hot-dry n = 31	Sign. test	Hot-wet n = 10	Cold-dry n = 23	Hot-dry n = 28	Sign. test
A. Active	*Overall*	21.0 (2.9)	44.9 (2.6)	36.7 (2.5	F = 6.7; p <0.05	46.5 (2.8)	50.2 (2.2)	39.6 (3.3)	NS
B. Foraging	Overall	21.0 (2.3)	43.2 (2.5)	35.9 (2.5)	F = 6.7; p < 0.05	36.2 (3.6)	42.9 (2.2)	30.1 (2.0)	F = 3.1; p = 0.05
	Searching	16.4 (2.3)	32.4 (3.1)	30.9 (2.5)	F = 5.1; p < 0.05	26.1 (3.9)	31.8 (2.6)	20.8 (2.0)	F = 2.4; p = 0.09
	Digging	2.2 (0.8)	8.4 (2.1)	4.8 (0.7)	F = 13.6; p < 0.001	6.9 (2.4)	8.2 (1.3)	6.4 (1.4)	Not significant
	Eating/Handle	1.9 (0.4)	1.8 (0.7)	1.8 (0.3)	Not significant	2.1 (0.6)	1.7 (0.3)	8.1 (0.4)	Not significant
C. Social	*Overall*	3.0 (2.8)	2.5 (2.9)	1.1 (0.5)	Not significant	5.8 (3.2)	10.5 (3.2)	12.3 (3.3)	Not significant
	Scent marking	1.9 (0.2)	1.8 (0.3)	0	Not significant	2.5 (1.2)	1.8 (0.3)	1.6 (0.3)	Not significant
	Travel	0	0	0	Not significant	4.1 (3.0)	3.5 (0.8)	5.3 (1.4)	Not significant
	Interactions	3.6 (2.8)	3.5 (2.6)	1.9 (0.1)	Not significant	2.2 (0.7)	7.3 (3.2)	6.8 (3.1)	Not significant
D. Other	*Overall*	2.1 (0.2)	2.0.	2.0 (2.5)	Not significant	2 (0.9)	2.0 (0.1)	6.8 (0)	Not significant
	Grooming	2.0 (0.1)	1.8 (0.9)	1.8 (0.1)	Not significant	0	2.1 (0.1)	1.8 (0.3)	Not significant
	Sand bathing	1.7 (0.3)	1.8 (0.4)	1.8 (0.2)	Not significant	2 (0.9)	2.1 (0.3)	2.0 (0.5)	Not significant
E. Resting	*Overall*	75.0 (3.4)	51.9 (3.0)	63.3 (2.5)	F = 3.7; p < 0.05	53.5 (2.8)	40.0 (0.9)	49.5 (3.2)	Not significant
	In hole	75 (3.4)	51.9 (2.1)	63.3 (2.5)	F = 3.7; p < 0.05	42.0 (5.7)	31.0 (3.2)	45.8 (3.3)	Not significant
	Above ground	0	0	0	Not significant	7.0 (3.8)	6.6 (2.3)	3.6 (1.3)	Not significant

Table 3.2 Results of significance tests (two-sided, two sample t-tests) comparing intersexual differences in the daily proportion of time spent in different activities.[1]

Behaviour category	♀Hot-wet vs. ♂ Hot-wet	♀ Cold-dry vs. ♂ Cold-dry	♀ Hot-dry vs. ♂ Hot-dry
Active	$t = -4.04$; $df = 30$; $p < 0.001$	Not significant	Not significant
Foraging	$t = -2.46$; $df = 30$; $p < 0.05$	Not significant	Not significant
Social	$t = -2.82$; $df = 30$; $p < 0.05$	$t = -3.48$; $df = 31$; $p < 0.05$	$t = -4.57$; $df = 57$; $p < 0.001$
Other	Not significant	Not significant	Not significant
Resting	$t = 2.42$; $df = 30$; $p < 0.05$	Not significant	Not significant

[1] = Proportions used in this analysis are presented in Table 3.1 and were arcsine transformed to achieved normality before analysis.

In the hot-dry and cold-dry seasons, males and females did not show intersexual differences in the proportion of time spent engaged in the time spent active, foraging, resting or engaged in other activities (Table 3.2). However, in the hot-wet season, males were active and foraged for significantly longer than females and, therefore, rested for proportionally less time (Table 3.1; Table 3.2).

Females always retreated to a burrow when resting, both during the day or night, but males were also seen to rest aboveground (4 –7 %; Table 3.1; Table 3.3), in the shade of *A. haemotoxylon* bushes and *B. albitrunca* trees during the day or curled up in a shallow scrape on the open dune slopes at night. It is assumed that female honey badgers spend the majority of their time in burrows resting, but mating and suckling of cubs also occurred in burrows and it was impossible to determine the relative proportion of time spent on these activities. Both males and females dug their own refuge burrows as well as adapting the burrows of other species i.e. aardvark *Orycteropus afer*, springhare *Pedetes capensis*, yellow mongoose *Cynictis penicillata* and other unidentified holes for their own use. Males and females differed significantly in their burrow use with males using the burrows of other species more frequently than digging their own refuge burrows, while females preferred to dig their own burrows and were relatively infrequently observed to utilize aardvark holes (Table 3.4).

3.4.1.2 Seasonal differences

In both males and females, significantly more time was spent foraging in the cold-dry season compared to the hot-dry and hot-wet seasons (Tukeys HSD for unequal N; females: hot-dry vs. hot-wet season, $p < 0.05$; cold-dry vs. hot-wet season, $p < 0.01$; males: hot-dry vs. hot-wet season, $p < 0.05$; cold-dry vs. hot-wet season, $p < 0.05$ Table 3.2). In both sexes this was associated (but not significant in males) with less time spent resting in the cold-dry season. In both sexes seasonal differences in foraging time were associated with increased search and

Table 3.3 Comparison of the types of refuge holes used by male and female honey badgers in the KTP.

Sex	Type of refuge hole			Sample size	Significance test
	Own hole	Aardvark hole	Other holes[1]		
♀	58 %.	20 %	23 %	222	$X^2 = 22.2$;
♂	39 %	37 %	22 %	417	$p < 0.001$

Table 3.4 A comparison of seasonal and daily differences in the length of the two active and two resting periods of the honey badger in the KTP.

Category	Percentage of 24 hr period					
Sex & Season	Active periods $\bar{x}$ (S.E.; n)[1]			Resting periods $\bar{x}$ (S.E.; n)		
	Morning	Evening	t-test[1]	Day	Night	t-test[1]
A. Males						
Hot-wet	10.0 (1.3; 14)	25.0 (1.6; 14)	t = 3.9; df = 18; $p < 0.001$	48.1 (0.9; 14)	23.4 (1.9; 14)	t = 5.6; df = 18; $p < 0.001$
Cold-dry	13.1 (1.7; 20)	21.6 (1.1; 18)	t = -4.2; df = 18; $p < 0.001$	28.6 (1.0; 20)	37.2 (0.9; 18)	Not significant.
Hot-dry	13.8 (1.4; 24)	19.2 (1.4; 24)	t = -2.1; df = 46; $p < 0.05$	36.1 (1.1; 24)	28.9 (1.9; 19)	t = 2.1; df = 41; $p < 0.05$
ANOVA	Not significant	Not significant		F = 24.3; $p < 0.05$	F = 6.17; $p < 0.05$	
B. Females						
Hot-wet	9.1 (0.9; 17)	14.3 (1.7; 17)	t = -2.4; df = 32; $p < 0.05$	41.1 (1.9; 13)	37.1 (2.8; 13)	Not significant
Cold-dry	9.7 (1.2; 18)	21.6 (1.8; 14)	t = -4.6; df = 30; $p < 0.001$	20.9 (2.7; 14)	43.5 (1.4; 14)	t = 4.7; df = 26; $p < 0.001$
Hot-dry	8.6 (1.3; 20)	16.4 (1.5; 20)	t = -3.54; df = 30; $p < 0.05$	41.3 (2.5; 19)	28.2 (1.4; 18)	t = 2.7; df = 35; $p < 0.05$
ANOVA	Not. significant	Not significant		F = 8.6; $p < 0.001$	F = 6.6; $p < 0.05$	

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[1] =The time spent in each period (min) was converted to a proportion of a 24 hr period and then arcsine transformed to achieve normality for use in parametric two-sample, two sided t-tests (Zar, 1999). Values were back transformed for presentation of results.

digging time in the cold-dry season (Table 3.1). In all seasons the amount of time recorded eating/handling prey was very low, particularly in females where it accounted for < 10 % of the total time spent foraging. This is due to a large number of small prey items, such as the barking gecko *Ptenopus garrulous* and scorpion *O. wahlbergii,* being eaten in less than a minute (Chapter 2; section 2.4.1.4). There were no seasonal differences in either sex in the proportion of time spent on any of the social activities, sand bathing or in the time spent grooming (Table 3.1).

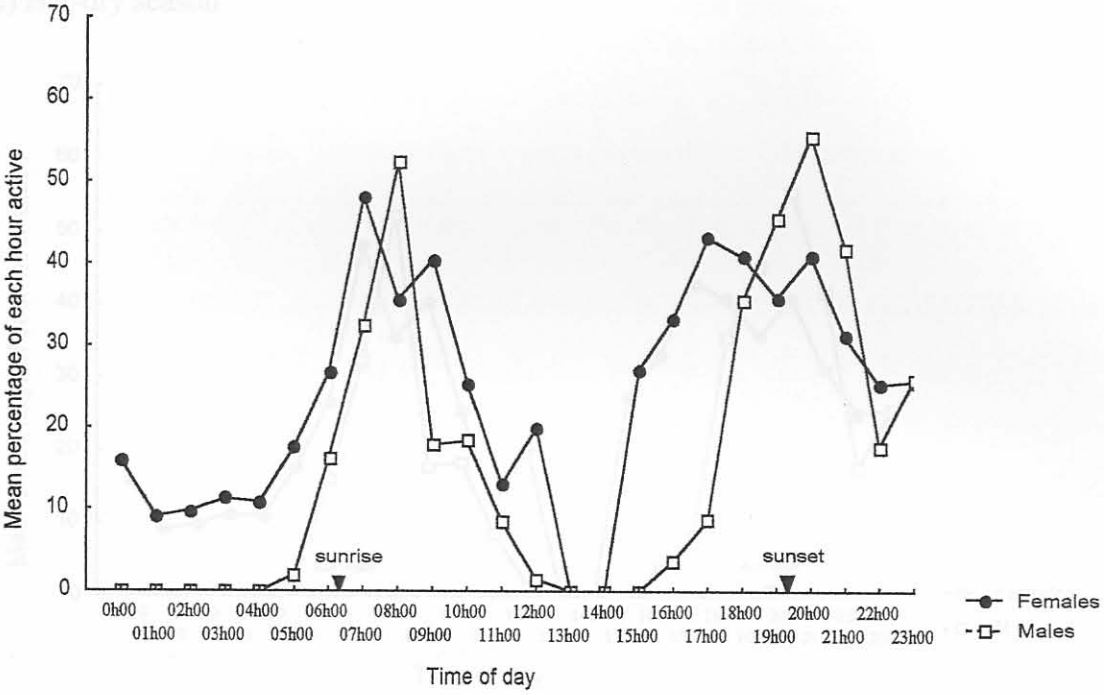
3.4.2. Activity patterns

3.4.2.1 Active periods

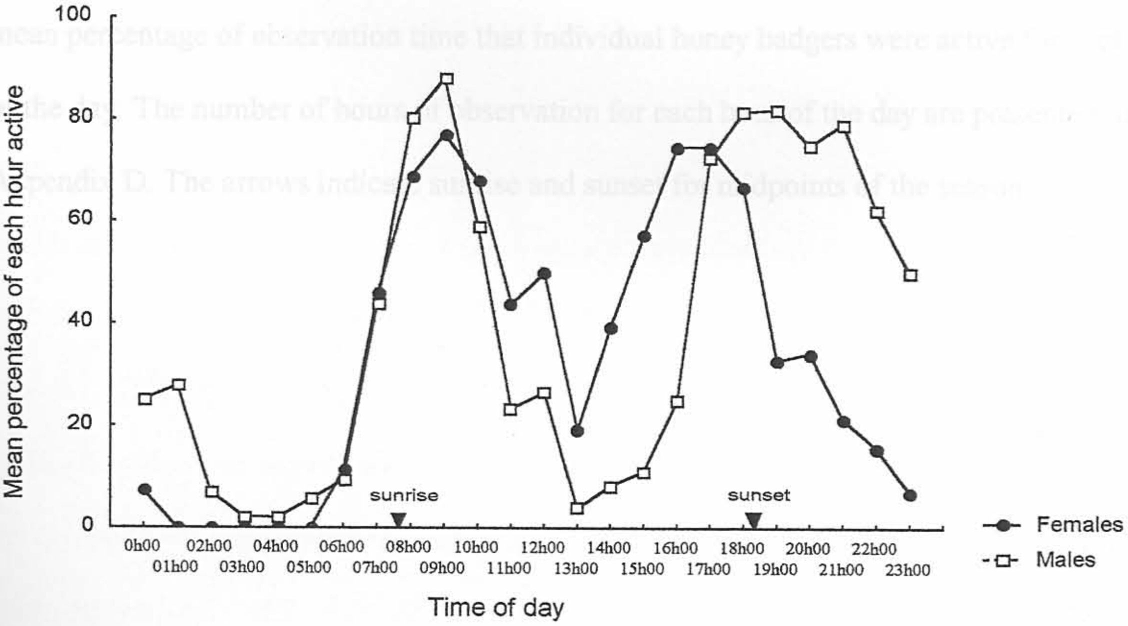
Male and female honey badgers showed a similar bigeminus (two peaked; Aschoff, 1966) activity pattern with the two daily peaks in activity in the morning and evening and a sharp decline in activity during the middle of the day in all seasons, but particularly during the hot-dry and hot-wet season (Figure 3.4a, b, & c). In all three seasons, the two daily peaks in activity occurred around sunset and sunrise (Figure 3.4a, b, & c).

A typical day could therefore be broadly divided into two active periods (morning & evening) and two resting periods (day & night), although there was considerable variation from day to day in both the onset of activity periods and their duration. In all three seasons in both sexes, the average duration of the evening active period was significantly longer than the morning active period, and there were no significant seasonal differences in the duration of either active period (Table 3.4). Neither the time of emergence from the hole in the morning nor the evening was directly correlated to the time of sunrise and sunset respectively. However, the average time of emergence from the burrow in the morning was later in the cold-dry season

a) Hot-wet season



b) Cold-dry season



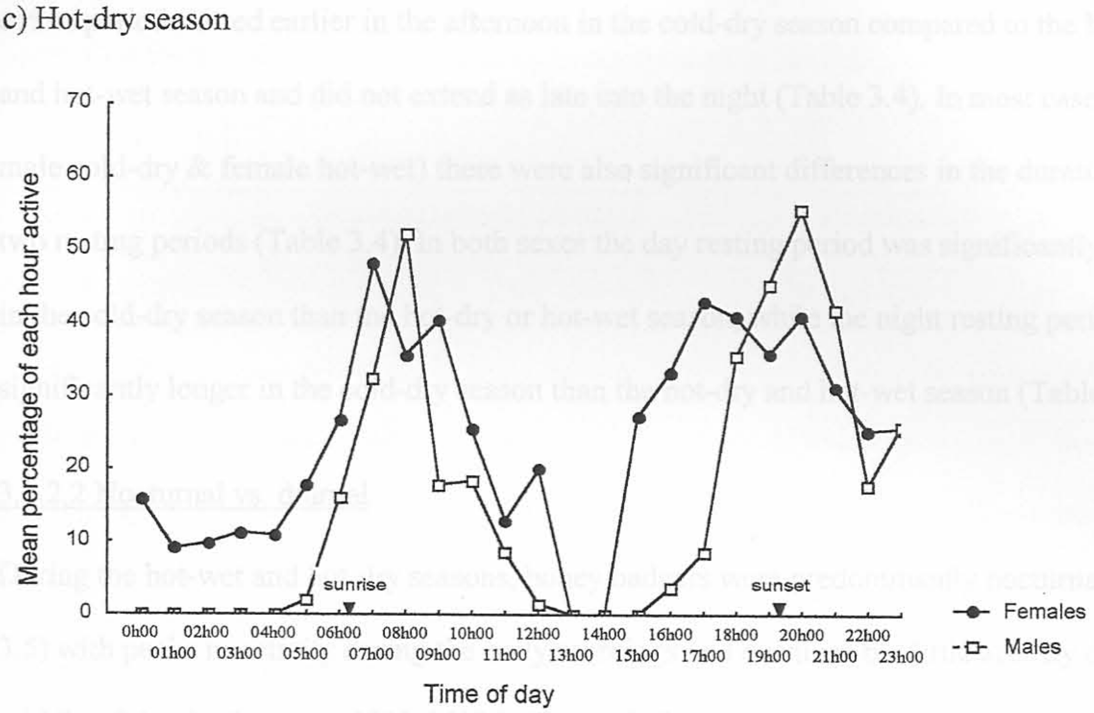

c) Hot-dry season

Figure 3.4 Daily activity schedule of male and female honey badgers in the hot-wet (a), cold-dry (b) and hot-dry (c) season showing the two-peaked pattern. Data were calculated as the mean percentage of observation time that individual honey badgers were active for each hour of the day. The number of hours of observation for each hour of the day are presented in Appendix D. The arrows indicate sunrise and sunset for midpoints of the season.

hot-dry and hot-wet season and the active period extended later into the day. The second daily active period started earlier in the afternoon in the cold-dry season compared to the hot-dry and hot-wet season and did not extend as late into the night (Table 3.4). In most cases (except male cold-dry & female hot-wet) there were also significant differences in the duration of the two resting periods (Table 3.4). In both sexes the day resting period was significantly shorter in the cold-dry season than the hot-dry or hot-wet season, while the night resting period was significantly longer in the cold-dry season than the hot-dry and hot-wet season (Table 3.4).

3.4.2.2 Nocturnal vs. diurnal

During the hot-wet and hot-dry seasons, honey badgers were predominantly nocturnal (Figure 3.5) with peaks in activity during the early mornings and evenings but little activity during the middle of the day between 0900-1600 h (Figure 3.4). These activity patterns were flexible and affected by local weather conditions as the honey badgers were seen foraging during the middle of the day on cool overcast days. In the cold-dry season, the honey badgers were active during the day (44.3 %) as well as at night (32,3 %). Foraging, social and other activities were all observed both during the day and night. However, females were only observed to move a den cub (< 3 month old; Chapter 7) to a new den during the night on one occasion (4 %; n = 27), although 15 den changes were observed during the hot-dry season, ten in the cold-dry and two in the hot-wet. On 16 occasions in the cold-dry season of 1999, a female (Af38) with a young cub of 4 months of age (J39) was observed to forage with the cub during the afternoon until sunset. At or just after sunset she would dig a den, leave the cub in the den and continue foraging for a further 2 – 3 hours at night before returning. On no occasion were cubs of 3 –4 months observed to forage with their mothers at night although

Table 3.5 Seasonal changes in the average time of emergence from and entry into the resting burrow for the two daily active periods of honey badgers in the KTP.

Sex and season	Morning active period		Evening active period	
	Time exit hole $\bar{x}$ [1](n)	Time into hole $\bar{x}$ (n)	Time exit hole $\bar{x}$ (n)	Time into hole $\bar{x}$ (n)
♂ Hot-wet	05h36 (18)	06h36 (25)	19h12 (18)	01h04 (21)
♂ Cold-dry	07h32 (54)	11h12 (66)	17h48 (42)	23h04 (48)
♂ Hot-dry	05h48 (44)	09h16 (54)	18h14 (33)	00h12 (30)
♀ Hot-wet	06h04 (28)	08h24 (40)	19h00 (28)	23h28 (32)
♀ Cold-dry	07h56 (25)	10h28 (28)	16h08 (25)	21h36 (23)
♀ Hot-dry	05h20 (52)	07h28 (58)	18h00 (48)	22h16 (32)

1 = A mean time of day was calculated by transforming times to angular directions (Section 3.3.2; Zar, 1999).

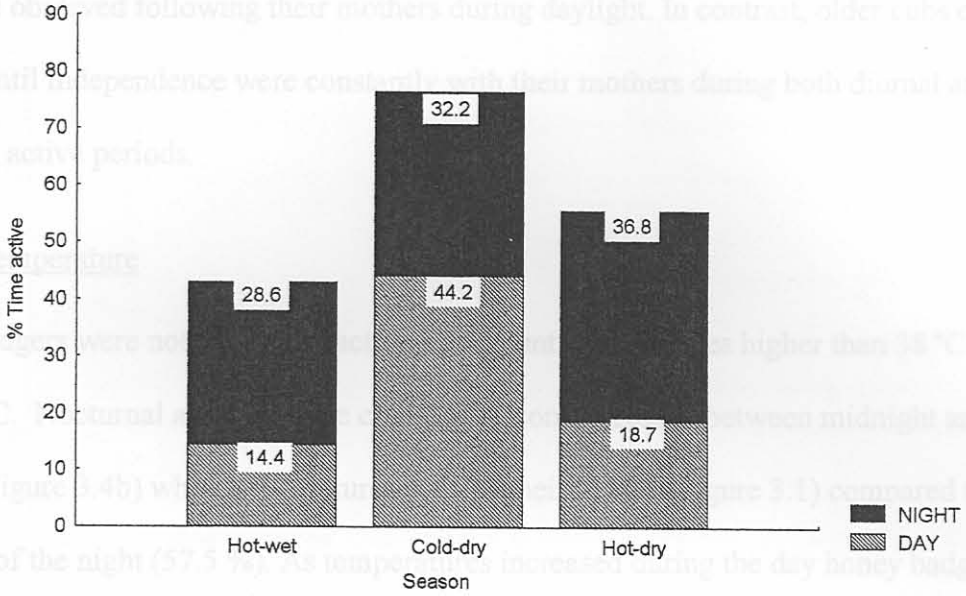


Figure 3.5 Seasonal differences in the relative nocturnal and diurnal activity of honey badgers in the KTP. To account for different amounts of observation time during the day and night, the time spent active was calculated as a percentage of the amount of time a honey badger were observed in each period (day or night) in each season.

they were observed following their mothers during daylight. In contrast, older cubs of 5 months until independence were constantly with their mothers during both diurnal and nocturnal active periods.

3.4.2.3 Temperature

Honey badgers were not seen to be active at ambient temperatures higher than 38 ^{0}C or lower than –2 ^{0}C. Nocturnal activity in the cold-dry season decreased between midnight and sunrise (07h30; Figure 3.4b) when temperatures were at their lowest (Figure 3.1) compared to the first half of the night (57.5 %). As temperatures increased during the day honey badgers were frequently seen to sand-bathe, i.e. throw sand onto their flanks and body with their front paws, while lying in the shade of vegetation. Seasonally, sand-bathing was most frequently observed in hot-dry season, and on a daily basis was most frequent during the middle of the day (Figure 3.6). Sand-bathing frequency was significantly correlated with temperature in the hot-dry (Spearman's rank correlation, $n = 24$, $r_s = 0.59$, $p < 0.05$) and cold-dry season ($n = 24$, $r_s = 0.82$, $p < 0.001$). In the hot-wet season, honey badgers were seldom active during the hottest period of the day (Figure 3.4) but rather retreated to a burrow, and as a result sand bathing was not often seen during this period (Figure 3.6). A high frequency of sand-bathing was frequently observed just before and after a honey badger retreated to or emerged from a day resting burrow. The percentage of time spent in a burrow during the day was significantly correlated with mean, maximum monthly temperature (Figure 3.7).

3.4.2.4 Prey activity

Overall there was no difference in the overall digging success of honey badgers during the day (43.2 %; n = 301 digging events) or night (42.6 %, n = 605). While there was also no significant difference between the percentage of large and small reptiles caught by day or at night, scorpions were predominantly caught during the day when they were in their burrows (inactive; Prendini, pers. comm.), and small mammals were predominantly caught at night

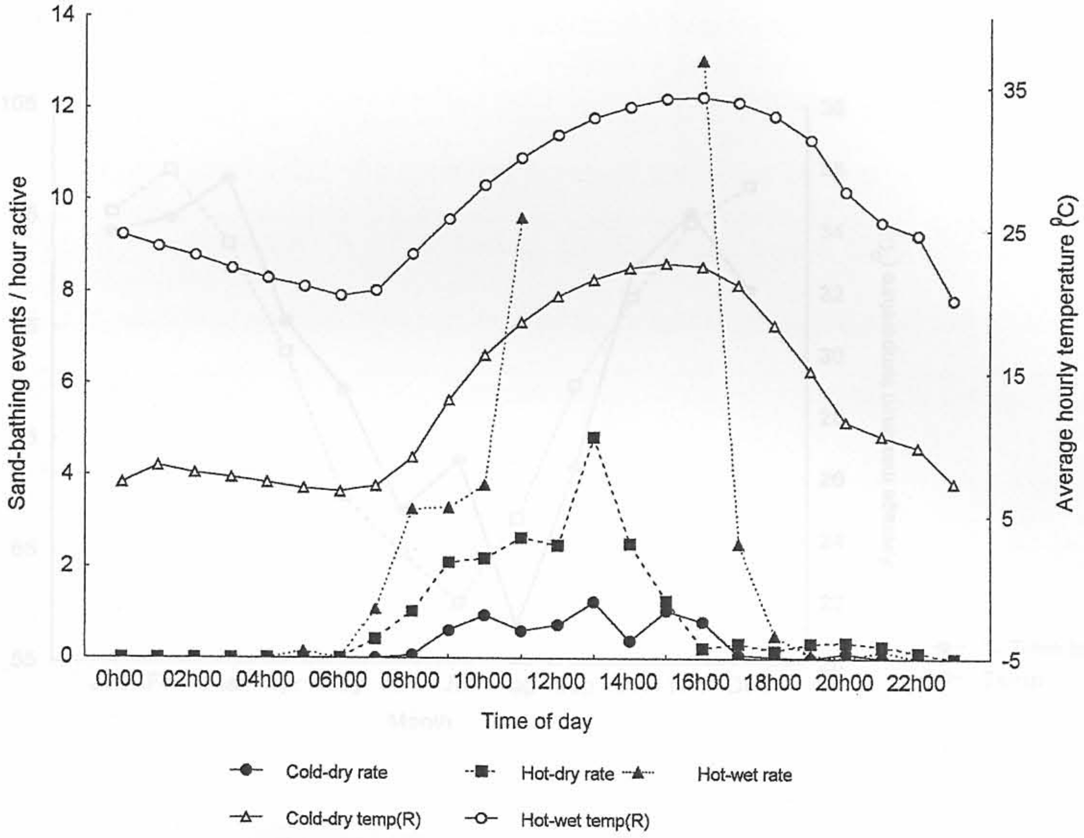


Figure 3.6 The frequency of sand-bathing events in honey badgers in the KTP and hourly changes in maximum temperature in the cold-dry and hot-wet season. Sand bathing frequency was calculated as the number of sand bathing events observed per hour of activity recorded for that hour of the day. The disjunction in the hot-wet season sand-bathing graph is due to honey badgers not being active (in a burrow) during the middle of the day in the hot-wet season.

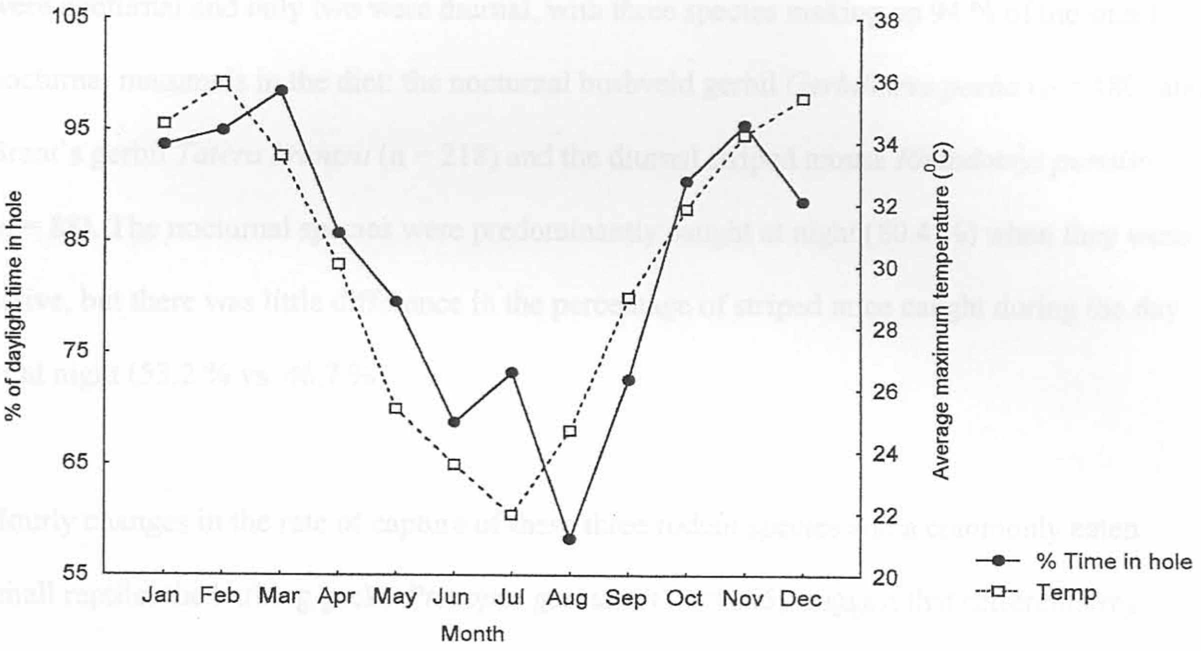


Figure 3.7 Relationship between average maximum temperature and the percentage of time honey badgers rest in a burrow during the daylight hours showing the increase in burrow use with increasing temperature. Spearmans rank correlation, $r_s = 0.79$, $p = 0.002$.

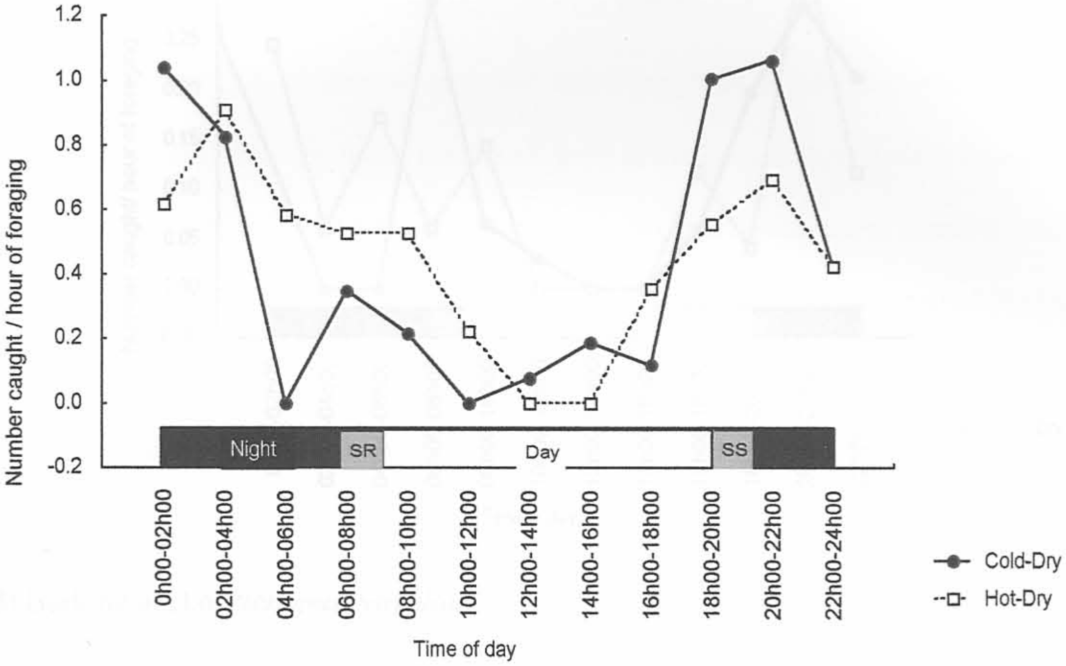
(Table 3.6). Of the nine small mammal species eaten by honey badgers in the KTP, seven were nocturnal and only two were diurnal, with three species making up 94 % of the small nocturnal mammals in the diet: the nocturnal bushveld gerbil *Gerbillurus paeba* (n = 480) and Brant's gerbil *Tatera brantsii* (n = 218) and the diurnal striped mouse *Rhabdomys pumilio* (n = 88). The nocturnal species were predominantly caught at night (80.4 %) when they were active, but there was little difference in the percentage of striped mice caught during the day or at night (53.2 % vs. 46.7 %).

Hourly changes in the rate of capture of these three rodent species and a commonly eaten small reptile, the barking gecko *Ptenopus garrulous* (n = 845), suggest that different prey species are eaten at different times of the day (Figure 3.6a-d). Since the hourly rate of capture of each prey species is calculated relative to the number of hours of foraging behaviour observed in each hour of the day, it is thus independent of the overall activity pattern of the honey badger. Both the bushveld gerbil and Brants gerbil were predominantly caught during the night (Figure 3.8 a & d) while the diurnal striped mouse (Figure 3.8b) was largely caught during the day in the cold-dry season. All three species showed peaks in capture around sunrise and sunset. Successful captures of the barking gecko showed a strong two-peaked pattern in both seasons with more diurnal captures in the cold-dry season compared to hot-dry season and with few captures between 20h00 – 04h00 in both seasons (Figure 3.8 d). Capture rates of the barking gecko by honey badgers were strongly correlated with hourly changes in temperature in the cold dry season (Spearman rank correlation; $R = 0.82$; $p < 0.001$; $n = 12$).

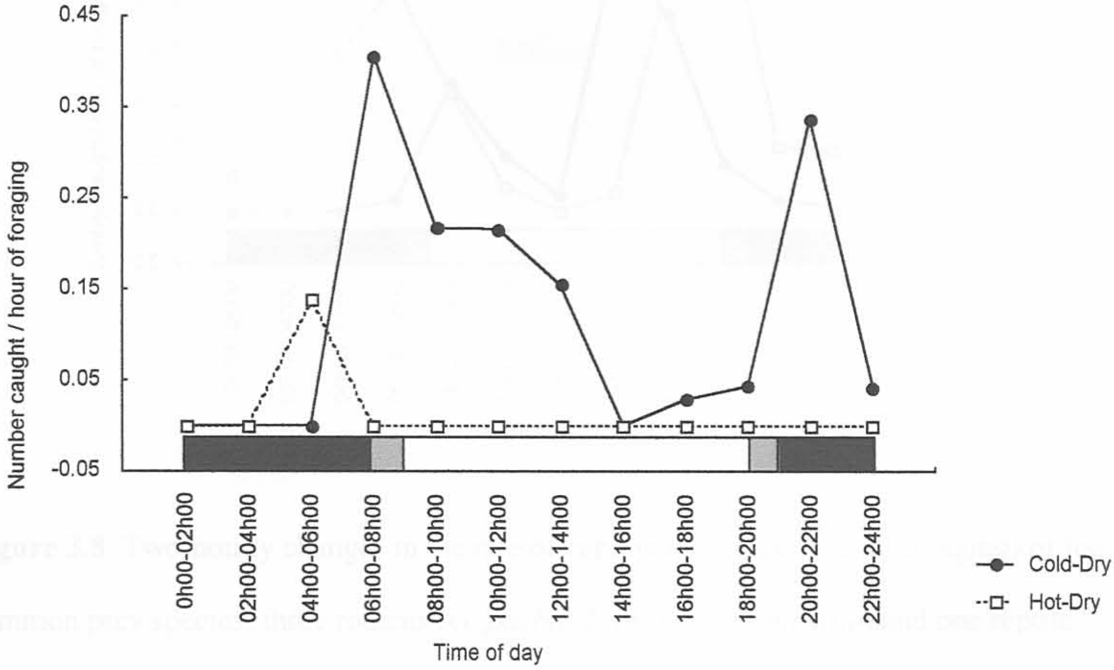
Table 3.6 Comparison of the percentage of the four most common prey categories caught by honey badgers during diurnal and nocturnal foraging. The percentages were calculated from the total number of prey items caught within each prey category during the study period in the KTP.

Time of day	Hrs. of Obs.	Percentage of prey category eaten			
		Small mammals (n = 1215)	Scorpions (n = 251)	Small reptiles (n = 1292)	Large reptiles (n = 181)
Day	1224	27 %	65 %	56 %	51 %
Night	1391	73 %	35 %	44 %	49 %
Binomial test		$p < 0.001$	$p < 0.001$	$p < 0.05$	Not sign.

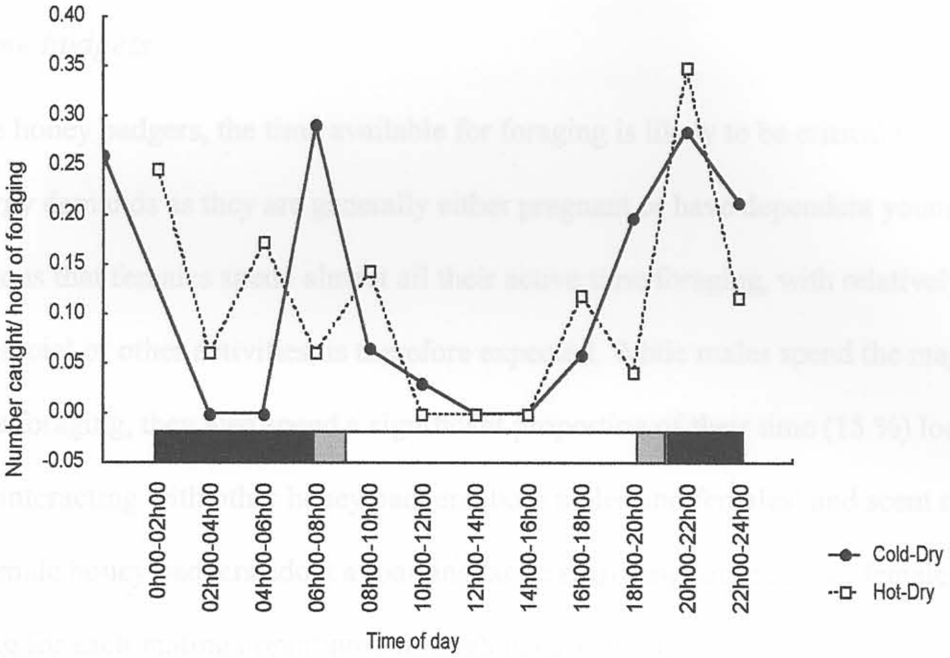
a) Bushveld gerbil *G. paeba*



b) Striped mouse *R. pumilio*



c) Brants gerbil *Tatera brantsii*



d) Barking gecko *Ptenopus garrulous*

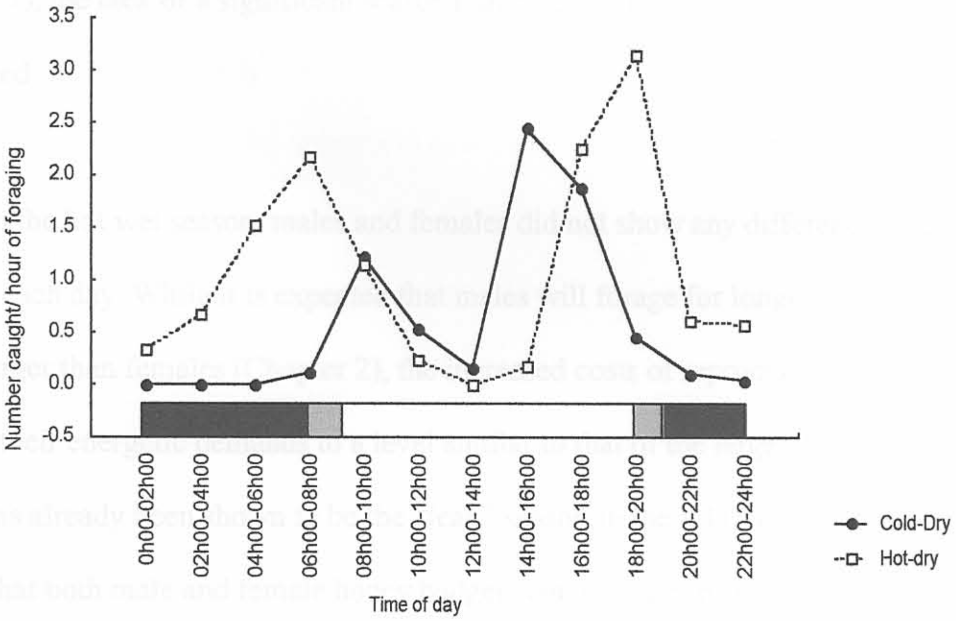


Figure 3.8 Two-hourly changes in the rate of capture (captures/ hour of foraging) of four common prey species; three rodents (*G. paeba, T. brantsii, R. pumilio*) and one reptile (*P. garrulous*) by honey badgers in the KTP.

3.5. Discussion

3.5.1 Time budgets

In female honey badgers, the time available for foraging is likely to be critical to meet their high energy demands as they are generally either pregnant or have dependent young. The observations that females spend almost all their active time foraging, with relatively little time spent on social or other activities, is therefore expected. While males spend the majority of their time foraging, they also spend a significant proportion of their time (15 %) looking for females, interacting with other honey badgers (both males and females) and scent marking. In the KTP male honey badgers adopt a roaming tactic searching for receptive females and competing for each mating opportunity through male-male interactions and scent marking (Chapter 7). Given that there is no breeding season for female honey badgers in the KTP (Chapter 7), the lack of a significant seasonal difference in the time spent on social activities is expected.

Except in the hot wet season, males and females did not show any difference in the time spent foraging each day. While it is expected that males will forage for longer since they are at least a third larger than females (Chapter 2), the increased costs of reproduction in females may increase their energetic demands to a level similar to that of the larger males. The cold-dry season has already been shown to be the "lean" season in the KTP (Chapter 2) and the data suggest that both male and female honey badgers compensate for the low dietary species richness and decreased consumption rates (Chapter 2) by increasing the time spent foraging each day. This behavioural compensation occurs in conjunction with prey switching and an increase in dietary diversity (Chapter 2). In both sexes the increase in foraging time was associated with a total increase in the time spent active (and less time spent resting), and not a decrease in the time being spent on "other" or social activities. As suggested by Gittleman and Thompson (1988), behavioural compensation therefore appears to provide an important tactic for meeting additional energy requirements. Time budgets of the honey badger therefore appear to be directly influenced by food availability and social organisation.

3.5.2 Activity schedules

The two peaked activity pattern found in the honey badger is not unusual and has been observed in a wide variety of carnivores (Aschoff, 1966; Kruuk, 1972). The activity patterns show crespuscular characteristics with increased activity during sunrise and sunset in all seasons.

In the KTP, the effect of human activity was thought to be minimal as the study animals were completely habituated to the research vehicle and the primary study site was in the central dune area away from tourist areas and camps. As predicted by Skinner & Smithers (1990), honey badgers are not strictly nocturnal in this wilderness area but are frequently active during the day. Light intensity appears to have little affect on foraging behaviour or foraging success of the honey badger, and since the sense of smell is its primary foraging sense not vision, light is probably relatively unimportant. The time of emergence from and entry into resting burrows was not correlated with the time of sunset or sunrise, and it is probable that the approximate time of emergence is primarily determined by physiological mechanisms (such as hunger), which govern the periodicity of sleep and activity (i.e. "the biological clock"; Neal & Cheeseman, 1996). Variations on the generalised pattern are likely to be due to local conditions such as temperature, rain and sandstorms. However, nighttime activity might have an associated cost in increased predation risk since the two main predators of the honey badger in the KTP i.e. lion *Panthera leo* and leopard *Panthera pardus* (Chapter 4) are largely nocturnal. The observation that females moved their cubs during the day, did not forage with young cubs at night, and were never observed to rest above ground supports this, but predation events were rarely observed and it was impossible to compare the risk of day and night foraging directly.

Dean *et al.* (1990) recently dismissed the well-known association between the greater honey guide *Indicator indicator* and the honey badger (Estes 1991; Attenborough 1998) as a myth stating as one of their reasons, the nocturnal activity of the honey badger compared to the diurnal activity of the honeyguide. In this study we have shown that at least in areas undisturbed by man, the honey badger is frequently active during the day, particularly in winter. This suggests that the association may exist in wilderness areas, but may have disappeared in more populated areas where the honey badger is largely nocturnal.

The timing of activity showed a strong seasonal shift from predominantly nocturnal activity in the hot-wet season to more diurnal activity in the cold-dry. Foraging theory predicts that predators should distribute their activity patterns to maximize net foraging benefit if foraging costs change as a function of the timing of the activity (Pyke *et al.*, 1977). This is supported to some degree in the bat-eared fox *Otocyon megalotis* in the KTP where similar seasonal shifts in activity patterns have been observed, and in this case the timing of activity patterns was shown to coincide with the above ground activity and availability of termites (their principal prey species; Nel, 1990).

The honey badger is a generalist and an opportunist and at least 65 different species have been identified as prey in the KTP (Chapter 2). If the daily activity schedules of prey result in them been differentially vulnerable to predation at different times of the day (Zielinski, 1988), then the honey badger will probably experience constant fluctuations in the vulnerabilities of different prey items. It has already been shown that the honey badger "switches" between different prey species on a seasonal basis in response to changes in prey availability (Chapter

2). The data presented here suggest that the honey badger also "switches" between different prey species during a single day with some prey caught predominantly at night (*G. paeba*), and others at sunset or sunrise (*P. garrulous*) or during the day (*R. pumilio*). Just as "prey switching" enables a honey badger to maintain its biomass intake on a seasonal level, "prey switching" on a daily basis may enable a honey badger to maintain its intake during a single foraging period. This is supported by no difference in the digging success of honey badgers foraging during the day or night, despite a wide variety of prey species eaten.

Samson & Raymond (1995) hypothesized that prey could be more easily detected when it is active and search time can be minimized if the predator hunts during prey activity bouts. For a predator such as the honey badger, which mainly locates its prey through smell and scent trails, the strong seasonal and daily activity patterns of prey species may substantially influence a honey badger's perception of their abundance (Chapter 2). On a seasonal basis the lower number of large reptiles (snakes) in the diet of honey badgers in the cold-dry season when they (the snakes) are inactive and increased numbers eaten during the warmer seasons when snakes are active despite no changes in actual abundance suggests that this is indeed the case (Chapter 2). However, on a daily basis the results are ambiguous as while some prey categories are more frequently caught when they are active (nocturnal gerbils), others are more frequently caught when they are in burrows and inactive (scorpions) and the remainder show no difference in the percentage caught during the day or night, whether they are active or inactive or above ground or in burrows (small reptiles, large reptiles, and diurnal rodents). This could not be tested directly both because there is little data available on the activity schedules of most prey items and because it was impossible to identify the prey species for unsuccessful digging attempts, and it was therefore impossible to determine changes in capture success at different times of the day for a particular prey species.

Zielinksi (1988) showed that small carnivores can be sensitive to within day variation in foraging cost, but that this is not the only criterion that influences seasonal foraging patterns. Given that the honey badger is a generalist that eats a wide variety of prey with differing activity schedules, it seems unlikely that prey activity alone is the driving force behind the seasonal shift in activity patterns of honey badgers in the KTP.

The decrease in activity during the middle of the day in the hot-wet and hot-dry seasons and between midnight and sunrise in the cold-dry season, and the correlation between the time spent in the burrow during the day and mean maximum monthly temperature, suggest that it is temperature that has the most important effect on a honey badger's activity schedules. This is expected given the extreme temperature fluctuations experienced in the arid KTP. Honey badgers appear to avoid extreme temperatures by using a burrow, and consequently shift their active periods to more nocturnal hours during the hot-wet and hot-dry season and more diurnal hours during the cold-dry season in order to satisfy their energy requirements. Similar shifts in activity due to temperature have been shown in a variety of mustelids and are taken to the extreme in animals that show winter aestivation or hibernation (Fowler & Racey, 1988; Dunstone, 1993; Neal & Cheeseman, 1994).

There is little doubt that the factors affecting the activity schedules of the honey badger are complex and likely to be interrelated and include predator risk, prey activity schedules, temperatures and disturbance by man. The ecological conditions experienced by the honey badger in its extensive range are highly variable, ranging from desert to savannah, to forest and dense woodland (Kingdon, 1989), and its time budgets and activity patterns are likely to change accordingly as has been shown in other carnivores (Dunstone, 1993; Samson & Raymond, 1995). However, in unprotected areas the honey badger appears to have shifted, almost completely, to nocturnal behaviour due to the effect of human activities and persecution (Skinner & Smithers, 1990). This "unnatural" shift may have negative effects on the honey badger due to increased foraging costs if some potential prey species are unavailable or more costly to catch during the night, increased energetic costs by limiting the use for behavioural thermoregulation, and possibly increased predation risk. In addition associations with diurnal species may go extinct i.e. the foraging associations with the diurnal pale chanting-goshawk *Melierax canorus* (Chapter 4) and the greater honey guide *I. indicator*.

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- Chapter 4 -

Interspecific interactions between the honey badger *Mellivora capensis* and other predators in the southern Kalahari: intraguild predation and facilitation.

4.1 Abstract

Visual observations of nine habituated honey badgers were used to investigate direct interspecific interactions between the honey badger *Mellivora capensis* and other sympatric carnivorous animals (mammals and birds) in the southern Kalahari. Foraging associations between honey badgers and seven other species (two mammals; five birds) were recorded, most commonly between the honey badger and the pale chanting-goshawk *Melierax canorus* and black-backed jackal *Canis mesomelas*. Goshawks and jackals benefit from the association by increased hunting opportunities and intake rate. In addition, chanting-goshawks show increased strike success and an expanded prey base when hunting with honey badgers compared to hunting alone. The honey badger does not show any significant differences in capture success, intake rate or predator vigilance when foraging in association compared to foraging alone. However, the jackal/badger association resulted in a significant decrease in the number of prey caught above ground by honey badgers (5 % of its prey overall), and this may have costs for honey badgers in the cold-dry season when prey availability is low and the foraging association is most common. Interspecific aggressive interactions could be predicted by relative body size and were largely asymmetrical. Intraguild predation was common and all mammalian carnivores smaller than the honey badger are prey items, as are the young of medium sized carnivores. The large carnivores, with the exception of the brown hyaena *Hyaena brunnea* and cheetah *Acinonyx jubatus,* prey on honey badger adults and cubs, while cubs are also killed by the black-backed jackal.

4.2 Introduction

The relationships between sympatric carnivorous animals are complex and may involve exploitative and interference competition (Cooper, 1991; Mills & Biggs, 1993; Creel *et al.*, 2001), intraguild predation (Creel *et al.*, 2001), as well as interspecific feeding associations where an individual of one species intentionally approaches an individual of another species and thereby gains some foraging advantage (Dean & Macdonald, 1981; Packer & Ruttan, 1988; Ellis *et al.*, 1993). While evidence for exploitative competition between mammalian carnivores remains elusive, direct interspecific aggression (interference competition) has been observed in a wide variety of mammalian carnivore species (Mills & Biggs, 1993; Palomares & Caro, 1999; Macdonald & Thom, 2001). The aggressive interactions may have a significant effect on the population dynamics of the subordinate competitor, particular in the case of intraguild predation, where two species compete for the same prey, but one species also preys on the other (Holt & Polis, 1997; Palomares & Caro, 1999; Creel *et al.*, 2001).

While interspecific interactions between large mammalian carnivores have been fairly well studied, particularly in Africa (Schaller, 1972; Mills, 1990; Mills & Biggs, 1993; Caro, 1994; Mills & Gorman, 1997), less information is available on the relationships between the smaller to medium sized carnivores (Mills *et al.*, 1984). The honey badger *Mellivora capensis* is a medium sized (6 – 12 kg) generalist carnivore that has not been well studied. Since nineteen mammalian carnivore species, excluding the honey badger, occur in the southern Kalahari, it is expected that these carnivores will interact with the honey badger in a variety of ways.

Despite its small size, the honey badger is commonly reported to have no enemies, aside from man, primarily due to its formidable threat display, strength and aggressiveness (Skinner & Smithers, 1990; Estes, 1992). Eaton (1976) suggested that these defensive attributes and the honey badger's striking colouration have resulted in Batesian mimicry by infant cheetah *Acinonyx jubatus* of adult honey badgers. The long, white back hair of cheetah cubs might mimic the appearance from above of honey badger adults and thus protect the cheetah cubs from predation, especially by raptors.

The honey badger is of particular interest as there are anecdotal accounts of a foraging association between it and the black-backed jackal *Canis mesomelas* and pale chanting-goshawk *Melierax canorus* in the more arid regions of South Africa (Cooper, 1974; Lombard, 1989; Mills *et al.*, 1984), Namibia (Paxton, 1988) and Botswana (Nelson & Nelson, 1987; Borello & Borello, 1986). It is generally agreed that jackals and chanting-goshawks catch fleeing rodents that escape while a honey badger is digging (Mills *et al.*, 1984; Dean *et al.*, 1990) but the possible benefits or costs to a honey badger are unclear.

It has been suggested that the goshawks indicate the presence of rodent burrows to the honey badger (Cooper, 1974; Dean & Macdonald, 1981; Borello & Borello, 1986). This suggests that the association might be an example of facultative mutualism, with both individuals gaining a foraging advantage although each individual can also forage alone (Rasa, 1983). Alternatively, the associating individuals might be stealing food from the honey badger i.e. kleptoparasitism (Cooper, 1991; Caro, 1994; Gorman *et al.*, 1998; Creel *et al.*, 2001), or the association may have no negative or positive effect on the honey badger i.e. commensalism (Ellis *et al.*, 1993). While commensalism and kleptoparasitism are relatively common, the relationship between the dwarf mongoose *Helogale undulata* and the Eastern yellow-billed hornbill *Tockus flavirostris* is the only verified example of facultative mutualism between two predators (Rasa, 1983). In this association the hornbill feeds on insects, especially locusts, flushed by the mongoose in return for giving warnings of specific avian predators, including those relevant only to mongooses (Rasa, 1983; Kemp, 1995).

Negative interactions such as competition, predation (particularly intraguild predation) and kleptoparasitism can adversely affect the population growth rate (Laurenson, 1995; Carbone *et al.*, 1997; Palomares & Caro, 1999; Creel *et al.*, 2001) and energetic intake of the victim (Cooper, 1991). Alternatively, a mutualistic or commensalistic foraging association may increase the population growth rate of one or both species through increased energetic returns, increased breeding success and/or increased vigilance (Rasa, 1983).

The aim of this chapter is to investigate these direct interactions between the honey badger and other species and to assess the possible negative or positive affects of these interactions on the honey badger and *vice versa*. Particular attention is given to the foraging association between the honey badger, pale chanting-goshawk and black-backed jackal.

4.3 Study area and methods

4.3.1 Study area

The project 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 and neighbouring Gemsbok National Park, Botswana.

It is a semi desert region and is described by Acocks (1988) as the western form of Kalahari Thornveld with a very open savanna of *Acacia haemotoxylon, Acacia erioloba* and desert grasses. This study was primarily conducted in the central dune area, which is characterized by medium to high dunes on reddish sands where *A. haemotoxylon* appears in a shrublike form with occasional *Boscia albitrunca* and *A. erioloba* trees. Dune areas are interspersed with slightly undulating open plains areas, with similar plant composition but with no *B. albitrunca* trees, and pans and yellowish sands, which support shrub veld of *Rhigozum tricophorum* and *Monechma sp* (Van Rooyen *et al.*, 2001).

4.3.2 Data collection

Nine radio implanted, adult honey badgers (five females with five cubs, four males) were habituated to the vehicle until they could be followed without any obvious influence on their foraging behaviour. Detailed capture, radio marking and habituation techniques are presented in Appendix A. Selected animals were followed continuously for observation periods ranging from one to twelve days ($\bar{x} = 4$, n = 91) with an additional 57 short observation periods (less than 24 h) ranging from 45 min to 20 h. Over the course of the study 5811 h were spent with these honey badgers (Appendix B). A spotlight was used for night observations.

During all observations, honey badgers and other species were observed from the roof of a vehicle approximately 10 - 30 m away depending on visibility and grass height. During continuous observations certain activities were timed to the nearest minute with a digital stopwatch and the success of each digging attempt, position of prey capture (in hole or above ground), and prey type were recorded. Detailed analysis of the diet and foraging behaviour of honey badgers in the KTP from visual observations are presented in Chapter 2, with information on activity schedules in Chapter 3.

Mammalian carnivores in the KTP were divided into three size classes: small (<1 kg), medium (1-12 kg) and large (>12 kg), with the honey badger a member of the medium size class (females: 6.2 kg; males: 9.2 kg; Chapter 2). The relative density of medium and large mammalian carnivores within the study area were assessed through spotlight counts and spoor transects. Spotlight counts were conducted during February – March 1996 from a vehicle along roads in the dunes (370 km; 18.4 h) and rivers (565 km; 24.5 h) in the KGNP. Transects were conducted from an hour after sunset until 23h30 with the aid of a 400 000 candle power spotlight and all carnivores were counted. A fixed length spoor transect of 30 km along a dust road through the central study area was monitored in the early morning at regular intervals during the study period (N = 20). The spoor of each carnivore, which had crossed the road during the previous night was identified with the aid of a Khomani-San tracker. Data were analyzed as the presence or absence of spoor from each species on the transect.

Basic data on the activity schedules and diets of mammalian carnivores and other associating species were obtained from the literature, where possible from the KTP or similar semi-arid habitats i.e. small to medium sized carnivores (except the canids): Mills *et al.*, 1984; Skinner & Smithers, 1990; bat-eared fox *Octocyon megalotis*: Nel, 1990; Cape fox *Vulpes chama*: Nel, 1984, black-backed jackal *Canis mesomelas*: Ferguson, 1980; Nel, 1984; Ferguson *et al.*, 1988; large carnivores: Mills, 1990. For the African wild cat *Felis lybica* and small-spotted genet *Genetta genetta*, prey species were obtained from data on stomach analysis in Botswana (Skinner & Smithers, 1990). Visual observations of hunting behaviour in the little Karoo were used for the pale chanting-goshawk *Melierax canorus* (Malan & Crowe, 1997) and pellet analysis for the owls (Steyn, 1982).

4.3.3 Data analysis

After Minta *et al.* (1992), honey badgers and individuals of other species were considered to be interacting when either's attention was focused on the other's activity. During aggressive interactions, the interaction ended either when one individual was killed, or when both individuals were no longer focused on each other. A foraging association was considered to begin as soon as the associating species appeared to be following a foraging honey badger's movements and ended when this individual lost interest in the interaction and moved off.

Both qualitative and quantitative information were used to assess interactions. For each interaction, each species' response to the others presence was recorded assuming that behaviour that initiates or maintains the association is evidence that the net outcome for the behaving animal is likely to be neutral or positive, while behaviour that tends to avoid or terminate the association is evidence that the net outcome is likely to be negative (Minta *et al.*, 1992). During foraging associations in particular, any behaviour or vocalizations that suggested coordinated hunting or non-hunting advantages of the association, for either individual; i.e. increased predator vigilance, were described.

Data were calculated as the relative percentage of time honey badgers were observed interacting with each of the other species i.e. the time the two species were observed together as a percentage of the total time honey badgers were observed active during the study. For diurnal associating species this was calculated using only the number of hours honey badgers were observed active during the day. Interaction periods were divided into spot observations (< 5 min) where the associating species were obviously affected by the presence of the vehicle and moved off almost immediately and sample observations of > 5 min. The frequency of occurrence of an association was calculated as percentage of observations where an associating species was with a foraging honey badger at the start of an observation period. This is termed "initial sightings" in the text.

For the pale chanting-goshawk and black-backed jackal, the type of prey caught, hunting success, and hunting rate (g / h) when foraging with a honey badger were calculated and compared with data from the literature when hunting alone (Ferguson, 1980; Malan, 1998; section 5.2.2.3). The digging success (percentage of digging events that resulted in successful capture) and intake rate (g / foraging min) of honey badgers when foraging with and without black-backed jackals and pale chanting-goshawks in attendance, were compared. Non parametric chi-squared analysis was used to compare seasonal differences in the frequency of occurrence of associations with Fishers exact test used to analyze 2 x 2 contingency tables as suggested by Zar (1999). Parametric two-sample, two-sided t- tests were used to compare the intake rate and capture success (proportions arcsine transformed; Zar, 1999) of the honey badger when foraging with and without associating species.

4.4 Results

4.4.1 Overview

Honey badgers were observed to interact directly with 14 of the 20 mammalian carnivore species that occur in the KTP (Table 4.1). Interspecific interactions were divided into three categories: foraging associations, aggressive (predator-prey) and neutral interactions (Table 4.1).

The results of the spoor and spotlight counts suggest that the black-backed jackal is the most common medium to large mammalian carnivore in the KTP (Table 4.2) and it was also the most common carnivore seen to interact with honey badgers (Table 4.1). The small spotted genet was only observed during the river spot light count and this is likely to be due to the low availability of trees in the dune areas (Table 4.2).

Table 4.1 Type and frequency of interspecific interactions observed between honey badgers and other mammalian carnivore species in the southern Kalahari from direct observations and from tracking spoor. Interactions are ranked in ascending order of the mass of associating species, provided by data from the literature (references in section 4.2.3.).

Species	Mass (kg)	Interactions with honey badgers		
		Category	Type	Interactions^2
Small				
Yellow mongoose *Cynictis penicillata*	0.6	Aggressive	Predation attempts by honey badgers (adults & juv.)	30
Slender mongoose *Galerella sanguinea*	♂ 0.5 ♀ 0.4	Aggressive	Predation attempts by honey badgers (adults & juv.)	1
Suricate *Suricata suricatta*	0.7	Aggressive	Predation attempts by honey badgers (adults & juv.)	3
Polecat *Ictonyx striatus*	♂ 0.9 ♀ 0.6	Aggressive	Predation attempts by honey badgers (adults & juv.)	3
Medium				
Cape fox *Vulpes chama*	3	Aggressive	Predation attempts by honey badgers (juv.)	5
			Aggressive defense of cubs	26
Bat-eared fox *Otocyon megalotis*	3	Aggressive	Predation attempts by honey badgers (juv.)	2
			Aggressive defense of cubs	3

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Table 4.1 (cont)

Species	Mass (kg)	Interactions with honey badgers		
		Category	Type	Interactions
African Wild Cat *Felis lybica*	♂ 5	Aggressive	Predation attempts by honey badgers	2
	♀ 4	Foraging	Foraging association	8
Aardwolf *Proteles cristatus*	9	Aggressive	Aggressive display	7
Black-backed jackal *Canis mesomelas*	12	Aggressive	Predation attempts by honey badgers (juv.)	19
			Predator of honey badgers (juv.)	3
		Foraging	Foraging association	137
<u>Large</u>				
Leopard *Panthera pardus*	42	Aggressive	Predator of honey badgers (adult & juv.)	1
			Threat display	2
			Avoidance	1
Brown hyaena *Hyaena brunnea*	39	Neutral	Scavenge honey badger carcass	1
			Neutral	9
Cheetah *Acinonyx jubatus*	♂ 54	Neutral	Neutral	1
	♀ 43			
Spotted hyaena *Crocuta crocuta*	♂ 57	Aggressive	Threat display	1
	♀ 71		Avoidance	2
Lion *Panthera leo*	195	Aggressive	Predator of honey badger(adults & juv.)	3
			Threat display	1
			Avoidance	4

Table 4.2 Relative abundance of medium and large carnivores in the central dune area of the KTP as determined from spotlight counts in dune and river habitat and a repeated spoor transect (n = 20) of 34 km through the study area. Ranked in descending order of body mass.

	Spotlight transects (936 km)				Spoor transects	
Carnivore species	Dunes (380 km)		Dry River (556 km)			
	Sightings / 100 km	% occur.	Sightings / 100 km	% occur.	Present[1]	% occur.
Lion	2.4	14.3	2	3.7	3	15
Spotted hyaena	0	0	0.9	1.5	1	5
Cheetah	0.5	3.2	0.9	1.5	2	10
Leopard	0	0	0.2	0.3	2	10
Brown hyaena	0	0	0.9	1.5	15	75
Caracal	0.8	4.8	0.5	0.9	17	85
Black-backed jackal	5.3	31.7	21.4	42.8	20	100
Aardwolf	0.3	1.5	0	0	3	15
Honey badger	0	0	0	0	7	35
African wildcat	1.6	9.5	1.8	3	16	80
Bat-eared fox	3.7	22.2	16.7	28.6	1	5
Cape fox	2.1	12.7	7.7	13.2	20	100
Small spotted genet	0	0	1.6	2.8	0	0

[1] Refers to the number of transects a species was recorded as present.

Since species were only recorded on a presence or absence basis on the spoor transects, this method underestimated the abundance of both group living species (i.e. bat eared fox and lion) and species with small home ranges such as the African wild cat. Spoor transects were, however, more successful than spotlight counts at locating honey badgers. The lack of success at locating honey badgers on spotlight counts may be due to its small eyes (poor eyeshine) and habit of moving away from a disturbance with their heads low seldom looking back.

4.4.2 Overall foraging associations

Overall seven species (two mammals and five birds) were observed to follow foraging honey badgers with the most common associations observed between honey badgers and pale chanting-goshawks (goshawks) and black-backed jackals (jackals). On 41 occasions both jackals and goshawks were observed with honey badgers at the same time, with as many as three goshawks and two jackals observed to follow a single foraging honey badger. Other associating birds included three owls (barn owl, marsh owl and spotted eagle owl) and one passerine (ant eating chat). Two of the associating species (pale chanting-goshawk and ant eating chat) are exclusively diurnal (Maclean, 1985), while the owls (Steyn, 1982) and African wild cat (Skinner & Smithers, 1990) are primarily nocturnal. The black-backed jackal and the honey badger are active during both the day and night (Ferguson, 1980; Chapter 3).

The honey badger catches most of its prey by digging (> 80 %; Chapter 2). Small mammals (< 100 g) and small reptiles (< 100 g) were the most common prey items caught by both sexes and contribute greater than 60 % of the prey eaten in all seasons. When digging for small mammals and small reptiles, honey badgers caught 55.4 % of the prey items in a hole, but 43 % of the prey items escaped above ground (Table 4.3) and it is these escaped prey items that are available for capture by associating species.

Table 4.3 Position of prey capture by female (n = 236) and male (n = 400) honey badgers when digging for small mammals (<100 g) and small reptiles (< 100 g), showing the percentage of prey that escaped and were therefore potentially available for capture by associating predators and honey badger digging success when foraging alone.

Outcome of digging event	Females		Males		Overall	
	Freq.	%	Freq.	%	Freq.	%
Prey caught in digging hole by honey badger (A)	112	47.6	240	60.0	352	55.4
Prey escaped hole & was caught above ground by honey badger (B)	18	7.3	29	7.3	47	7.3
Prey that escaped capture (C)	106	45.1	131	32.7	237	37.3
Prey available for associating species (B + C)	114	48.5	160	40.0	274	43.1

Males and females differed significantly in the number of prey items caught in a hole ($\chi^2 = 6.4$; $p < 0.05$; Table 4.3) and more prey escaped when females were digging. Female honey badgers are therefore likely to be the most productive sex for associating species to follow. Overall honey badgers recaptured 16.3 % of the prey that escaped by chasing it above ground, but this represented only 7 % of the total small mammal and small reptile prey caught overall.

4.4.3 Honey badgers and pale chanting-goshawks

On 36 % of the initial daylight sightings of honey badgers (n = 319; section 5.2.2.3), chanting-goshawks were in attendance. Both adult and immature chanting-goshawks were observed to follow the honey badger with up to six individuals in attendance at one time ($\bar{x} = 2$). Chanting-goshawks were observed with habituated honey badgers for 111 h, or 15.8 % of the time honey badgers were observed to forage during the day. Interaction periods varied from 2 - 366 min (n = 194) with 66 spot observations (< 5 min) where the goshawk was obviously affected by our presence and flew off soon after we arrived and 128 sample observations with a mean duration of 52 min. Data from initial daylight sightings suggests that the foraging association is more common in the cold-dry season than the hot-dry or hot-wet season ($\chi^2 = 26.3$; df = 2; $p < 0.01$; Table 4.4) and more commonly observed with female honey badgers (46 % of 163 initial sightings) than males (25 % of 156 sightings; Fishers exact test; $p < 0.001$).

Of the 71 prey items observed to be caught by chanting-goshawks when foraging with honey badgers, 39.4 % were small reptiles (n = 26: barking gecko *Ptenopus garrulous*; n = 2: skink *Mabuya occidentalis*) and the remaining 61 % were small mammals (n = 20: hairy footed gerbil *Gerbillurus paeba;* n = 4: Brants gerbil *Tatera brantsii;* n = 19: striped mouse *Rhabdomys pumilio*.)

Table 4.4 Seasonal differences in the number of hours and relative percentage of time black backed jackals and pale chanting-goshawks were observed with honey badgers. The data for each season are pooled over the three years study period (1996 –1999).

Category	Seasons			
	Hot wet	Cold-dry	Hot-dry	Overall
A. Pale chanting-goshawk *M. canorus*				
Number of hours honey badgers were observed active (day)	184	220	314	718
Relative percentage of observation time goshawks were with honey badgers	11.3 %	23.0 %	12.3 %	15.8 %
Number of initial daylight sightings of honey badgers[1]	79	110	130	319
Percentage of daylight sightings where goshawks were present.	21.5 %	55.5 %	30.7 %	36 %
B. Black backed jackal *C. mesomelas*				
Number of hours honey badgers observed active (day + night)	276	596	796	1668
Relative percentage of observation time jackals were with honey badgers.	5.5 %	8.3 %	4.1 %	6 %
Number of initial sightings of honey badgers (day + night)[1]	121	136	169	426

[1] = Initial sightings refers to the start of a honey badger observation period.

The strike success of chanting-goshawks when hunting vertebrate prey in association with honey badgers was 58. 4 % (n = 95 strikes), compared to 10 - 14 % when hunting alone or 21 – 25 % when hunting with conspecifics in a similar environment (Malan, 1998). The rate of successful strikes when hunting with honey badgers in the KTP (0.89 ± 1.05 strikes / h; n = 34 observation periods) was also higher than the successful strike rate of adult chanting-goshawks hunting alone (0.15 ± 0.24; n = 84; Malan, 1998), but this difference was not significant (two-sample; two-sided t-test). Overall goshawks caught 60.6 % of the prey that escaped due to a honey badger's digging efforts (Table 4.5) and on average the consumption rate of chanting-goshawks when foraging in association with honey badgers was 22 g / h. The overall number of prey items caught above ground by honey badgers decreased from 16 % to 13 % when pale chanting-goshawks were present (Table 4.5), but this decrease was not significant and represented a total loss of less than 2 % of overall prey items. There was also no difference in the overall digging success or intake rate of a honey badger hunting alone or in association with a chanting-goshawk (Table 4.6).

On all occasions chanting-goshawks initiated an interaction by flying in and perching alongside foraging honey badgers and on three occasions they were observed to fly in and perch within 20 m of a resting burrow at least an hour before a honey badger emerged. Chanting-goshawks live in family groups and are strictly territorial (Malan & Crowe, 1996) and observations suggested that individual goshawks stopped following a honey badger when a territory boundary was reached.

Table 4.5 Percentage of available prey items caught by honey badgers, pale chanting-goshawks and black-backed jackals when foraging in association, where prey available refers to prey items that escaped above ground while honey badgers were digging.

Outcome of digging event	Honey badger + jackal	Honey badger + goshawk
Escaped prey caught by associating species (%)	68.9	60.6
Escaped prey caught by honey badger (%)	4.9	12.8
Escaped prey not caught (%)	26.2	26.6

Table 4.6 A comparison of the capture success (%) and intake rate (g / min) of male and female honey badgers foraging for small reptiles and small mammals in association with the black-backed jackals and pale chanting-goshawks and when foraging alone. The differences in capture success and intake rate of honey badgers when foraging with or without jackals or goshawks in attendance were not significant (two sided, two sample t-test[1]).

	Females $\bar{x}$ (S.E; n)			Males $\bar{x}$ (S.E; n)		
	Alone	With jackal	With goshawk	Alone	With jackal	With goshawk
Capture success [1+2] (%)	43 (1.4; 156)	41 (2.4; 14)	44 (3.4; 20)	46 (1.4; 128)	52 (8.5; 18)	49 (3.4; 17)
Intake rate (g / min)	0.8 (0.1; 84)	1.1 (0.2; 13)	0.5 (0.1; 10)	1.0 (0.1; 109)	1.5 (0.3; 11)	1.0 (0.1; 24)

[1] Proportions were arcsine transformed to normalize for t-test analysis, and back transformed for presentation.

[2] Capture success was calculated as the percentage of digging events that had a successful outcome (prey was caught) per observation period.

The chanting-goshawks frequently followed foraging honey badgers from high perches (commonly *B. albitrunca* trees) at least 50 m away, whilst also hunting independently. Once a honey badger began to dig, the chanting-goshawk would fly in and either stand on the ground within 1 - 2 m of the honey badger and follow on foot, or would perch alongside on low shrubs (e.g. *A. haemotoxylon)*.

When foraging with a honey badger, chanting-goshawks were heard to vocalize with a variety of calls ranging from a shrill shriek when striking at a prey item, to an excited cheeping when a prey item was observed, and a quieter, continuous cheeping or "murmuring" when perched. A similar quieter continuous cheeping is used between group members when no honey badger is present, particularly in response to a prey item or nest stick being brought in and its function may be to inform group members of intent (G. Malan; pers. comm.). The loud, high pitched cheeping heard in this study may simply be a louder form of the low continuous cheeping.

On seven occasions the honey badger looked up on hearing vocalizations from chanting-goshawks, particularly the high pitched cheeping and on four occasions approached the chanting-goshawk to investigate. A honey badger caught a prey item as a result of moving towards a chanting-goshawk on only one occasion. On this occasion the honey badger had entered a resting burrow but on hearing the nearby excited cheeping of the chanting-goshawk perched on the ground 2-3 m from the hole, the honey badger re-emerged and approached the chanting-goshawk, which was standing at a rodent burrow. The honey badger began to dig and caught a *G. paeba*. It is considered unlikely that chanting-goshawks consistently aid the foraging efforts of honey badgers by showing them where to dig. On only one occasion was a chanting-goshawk heard to give an alarm call in the presence of a honey badger and the honey badger did not respond. During capture honey badgers were ambushed on foot and caught in hand nets (n = 66; Appendix A) and chanting-goshawks were in attendance on 21 capture events. On all occasion the chanting-goshawks flew off before the honey badger was aware of any danger and did not appear to warn it.

4.4.4 Honey badger and black-backed jackal

On 16 % of the initial sightings of honey badgers (n = 426; night and day), black-backed jackals (jackals) were in attendance. Between one and four jackals were observed with a honey badger at one time ($\overline{x} = 1$). Jackals were observed with habituated honey badgers for 236 h comprising 156 observation periods ranging in duration from 2 – 847 min ($\overline{x} = 110$ min). This included 27 spot observations (< 5 min) and 129 sample observations (5 - 847 min). Unlike the association with the goshawk, the relationship between the honey badger and jackal was not simply a foraging one and the behaviour of the jackals during sample observations could be divided into foraging (n = 94 events, 98 h of observation), resting (n = 4 events, 135 h) and aggressive interactions (n = 12 events, 3 h). Foraging and resting behaviour are discussed in this section, while aggressive interactions are discussed separately (section 4.3.3). Overall jackals were observed with honey badgers for 6 % (98 h) of the time honey badgers were observed foraging. Data suggest that jackals were more frequently seen with honey badgers in the cold-dry season than the hot-dry or hot-wet season ($\chi^2 = 8.62$; df = 2; $p < 0.05$; Table 4.5) and more frequently observed with female honey badgers (22 % of 223 initial sightings) than males (11 % of 203 sightings; Fishers exact test; $p < 0.05$). The relative percentage of time jackals were observed with foraging honey badgers during each hour of the day ranged from 2.5 - 11.5 % (Figure 4.1), with no discernable preference for either nocturnal or diurnal foraging. On 24 occasions jackals rested in close proximity (2 – 15 m) to a honey badger's resting burrow for periods ranging from 48 – 847 min ($\overline{x} = 385$ min), waiting for the honey badger to emerge for the next foraging bout.

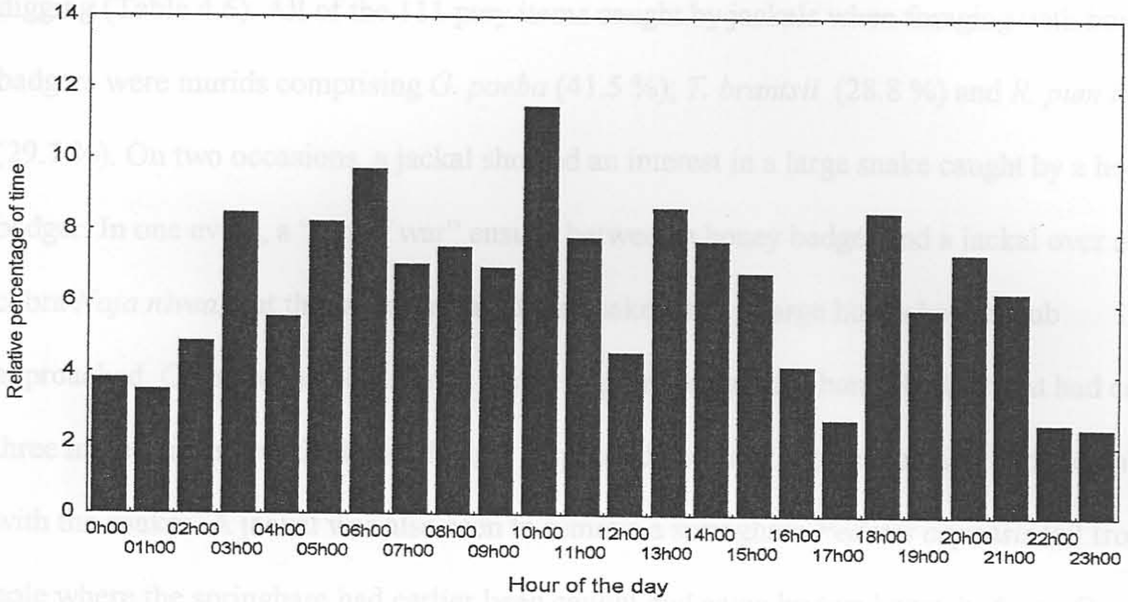

Figure 4.1 Percentage of time black-backed jackals were observed with honey badgers, relative to the number of hours honey badgers were observed foraging during each hour of the day, averaged over the study period (1996-1999).

Jackals were observed to catch 69 % of the prey that escaped whilst honey badgers were digging (Table 4.6). All of the 111 prey items caught by jackals when foraging with honey badgers were murids comprising *G. paeba* (41.5 %); *T. brantsii* (28.8 %) and *R. pumilio* (29.7 %). On two occasions, a jackal showed an interest in a large snake caught by a honey badger. In one event, a "tug of war" ensued between a honey badger and a jackal over a Cape cobra *Naja nivea,* but the jackal released the snake when a large honey badger cub approached. On a second occasion, a jackal approached a male honey badger that had caught three mole snakes, but the honey badger responded by growling and backing into the hole with the snakes. A jackal was also seen to remove a springhare *Pedetes capensis* tail from a hole where the springhare had earlier been caught and eaten by two honey badgers. On one further occasion, a jackal caught a striped polecat that had escaped from a hole where two honey badgers were digging but dropped it when the polecat released its scent. The polecat was then recaught and eaten by the honey badgers.

On average, a jackal caught 296 g / h when foraging with a honey badger. During one period of 212 minutes, a jackal caught 17 murids (715 g) that escaped due to the digging efforts of the honey badger and buried (cached) five prey items, and the honey badger caught seven murids and one small reptile (161 g). The jackal continued to follow the honey badger until she retreated to a burrow to rest and then slept within 10 m of the hole.

The number of prey items caught above ground by honey badgers decreased significantly ($\chi^2 = 11.2$, $p < 0.01$) from 16 % without jackals to only 5 % when jackals were present However, this represented only a 5 % decrease in the overall number of prey caught. There was no difference in the digging success or intake rate of a honey badger foraging with and without a jackal (Table 4.6), and there was little evidence to suggest that a honey badger and jackal actively cooperated when foraging in association, although on several occasions the presence of another predator waiting at possible rodent escape holes may have influenced the outcome.

In all cases a jackal initiated an interaction. Jackals traveled close behind, ahead or alongside (2 - 10 m) a foraging honey badger and stopped when a honey badger stopped to dig. On a few occasions, a honey badger appeared to be following the jackal for a short distance. On 42 occasions while being followed, the honey badger rushed aggressively at the jackal. These chases were less than 5 m and were frequently accompanied by a short rattle/growl by the honey badger. The chases occurred in response to a jackal being in the way, too close, or while catching a prey item. On no occasion did a honey badger make physical contact with a jackal, and the only effect of these chases was that the space between the jackal and the honey badger increased temporarily.

A jackal was observed to give a predator alarm call on two occasions when with a honey badger, and on both occasions the honey badger stopped to listen but then continued foraging. During capture (n = 52), at least one jackal was with the honey badger on nine occasions but were never heard to warn the honey badger of danger, and the honey badger did not appear to take any notice when the jackal ran off at the approach of the capture team.

4.4.5 Other associating species

Groups of up to eight ant eating chats *M. formicivoras* were observed to follow foraging honey badgers on 65 occasions for periods ranging from 2 - 130 min ($\bar{x} = 20$ min). They were observed with honey badgers for 3 % of the time honey badgers were observed foraging during the day. They flew in from as far as 200 m and followed the honey badger for distances up to 500 m from their nesting and roosting sites (holes in the roofs of aardvark

Orycteropus afer burrows). The chats perched on the ground within 1-2 m of a digging honey badger gleaning insects that were disturbed by the honey badger's digging efforts. On one occasion an individual caught and ate a barking gecko *P. garrulous* that escaped while the honey badger was digging. The honey badger ignored the chats during these associations although both adults and chicks are prey items (Chapter 2), and there appeared to be no obvious benefits or costs to the honey badger from this association.

Individuals of three species of owl (spotted eagle owl *Bubo africanus*: n = 7 observations; barn owl *Tybo alba*: n = 5; marsh owl *Asio capensis*: n = 3) followed foraging honey badgers at night on 15 occasions. While the owls were not observed to catch prey, it is likely that this was their intention since on five occasions they circled and swooped over a digging honey badger before landing on the ground within 5 m of the honey badger and followed the honey badger's foraging path. Similarly, the African wild cat *F. lybica* was also observed to follow honey badgers (two females, two males) at night on eight occasions but all interactions were of short duration (3 - 22 min). On all occasions African wild cats intently watched the digging actions of a honey badger from less than 5 m away, but were nervous of the vehicle. On no occasion did the honey badger display any aggression or interest towards the African wild cats, although both kittens and adults have been recorded as prey items (Chapter 2). It is considered possible that these two species forage in association when undisturbed as the diet of the two species overlaps considerably (African wild cat: Skinner & Smithers, 1990; honey badger: Chapter 2).

4.4.6 Intraguild predation and aggressive interactions

The adults and juveniles of the smaller mammalian carnivores, yellow mongoose, slender mongoose, suricate and the striped polecat are all prey of the honey badger, as are young Cape fox, bat-eared fox, and African wild cat (Table 4.1; Chapter 2).

Adult Cape fox, bat-eared fox and black-backed jackal were observed to bite and chase honey badgers that were in close proximity to or raiding dens (Table 4.1). On three occasions an aardwolf *P. cristatus* was observed to give its threat display (raising its mane and vocalizing with a hoarse bark) towards a honey badger that entered a den, and it is likely that aardwolf young are also prey of the honey badger. In most cases honey badgers ignored these attacks but were noticeably more nervous of black-backed jackals than of the other species.

On 14 occasions a jackal bit a honey badger adult and/or cub during a foraging association, and in all cases these brief attacks appeared unprovoked. Adults were bitten on the rump whilst they were digging and cubs were bitten when the adult females were occupied. In all cases the cubs alarm called, at which the adult females rushed at the jackal and the jackal backed off a few meters.

Longer duration aggressive interactions initiated by jackals (that were not associated with foraging associations) were observed on 19 occasions (5 - 48 min). These interactions consisted of repeated chasing, biting and harassing of a honey badger until it moved off. These interactions occurred predominantly in the hot-dry season (Sep-Dec; 68 %), with six (32 %) observations in the cold dry season (May-Aug) and none in the hot-wet season (Jan-Apr). This coincides with the breeding season of jackals in the KTP (Ferguson, 1980), and on two occasions (23/10/96 & 02/11/96) jackal dens with cubs were known to be within 100 m of the interaction. Honey badgers were not observed to eat jackal pups in the KTP, but this has been observed in Etosha (Hancock, 1999).

On one occasion a young adult male honey badger was repeatedly attacked and bitten by a jackal on the head and rump. The jackal ran towards the honey badger from 200 m with its ears flat and head low and the honey badger responded by lying down flat on the ground facing the jackal, vocalizing with a low rattle growl. After the second attack the honey badger approached the jackal and when within < 2 m, rolled onto his back, presenting his belly, with all four feet in the air. The jackal made no attempt to bite the honey badger in this position and lay down facing the honey badger. The honey badger was immediately attacked again once it got up and responded by again rolling onto its back. This rolling behaviour was observed on four occasions until the jackal ran off.

This behaviour was observed on one other occasion when the same honey badger responded to an aggressive interaction between two jackals by approaching the two jackals and lying on his back between the two individuals. Both jackals ignored the honey badger. More usually, honey badgers simply ran away from aggressive jackals but turned around to face the jackal if it attacked.

The honey badger is killed by lion and leopard and possibly spotted hyaenas in the KTP (Table 4.1). Of seven adult male honey badgers killed, three were thought to have been killed by large predators due to the presence of lion spoor around the remains and skull puncture wounds. Of the females, one was killed by a leopard, and signs (spoor, teeth marks on radios) suggested that the other two were also predated by a large predator. Three honey badger cubs were thought (from spoor and teeth marks) to have been killed by large predators, and on two of these occasions both the mother and the cub died. On four occasions a female honey badger with a <1 month old cub in a den was observed to aggressively chase a jackal 80 - 100 m away from the den. On two of these occasions the jackal put its head and shoulders into the den burrow while the female was foraging within 10 m of the den. This behaviour suggests that the black-backed jackal may be a predator of honey badger cubs.

Honey badgers avoided interactions with large predators (Table 4.1). On seven occasions honey badgers were observed to intensively smell the ground and grass stalks around the fresh tracks of lion (n = 4), leopard (n = 1) and spotted hyaena (n = 2). In all cases after smelling the spoor the honey badger changed direction, and in one case on smelling fresh lion spoor a male honey badger bolted into a nearby burrow and did not come out until the following day.

When avoidance was not possible, a honey badger's response to a large predator was one of "fight" rather than "flight". Its formidable close quarters predator defense consists of a threatening rattle-roar, pilo-erection, the release of scent from anal scent glands and a rushing movement towards the predator. This defense was observed to be successful at warding off leopard (n = 2; one observation was made by D & C Hughes pers comm.), lion (n = 1) and spotted hyaena (n = 1). During the spotted hyaena interaction, the honey badger initially lay flat and motionless in the grass on smelling the three hyaenas. When the hyaenas were within 2 - 3 m of the honey badger, he stood up, rushed at the hyaenas, released the scent, vocalized and then ran off. The hyaenas made no further attempt to pursue the honey badger. Similar interactions between both spotted hyaena and brown hyaena, and honey badgers have been observed in the KTP (Mills, 1990) and Central Kalahari Reserve (Owens & Owens, 1978). The thick, loose skin of the honey badger is thought to provide some protection against predator bites and enables a honey badger to twist around and bite the attacker. This was supported by observations of a female leopard, which fought with a 6 kg honey badger for 52 min before the leopard was able to deliver a killing bite to the throat.

Visual observations suggested that neither the brown hyaena nor cheetah are predators of the honey badger, although on two occasions honey badger carcasses were found in brown hyaena dens (Table 4.1). On the eight occasions that honey badgers and brown hyaenas were observed to interact, the honey badger was not seen to use the threat display. On all occasions the brown hyaena approached the honey badger and then changed direction and moved off.

4.5 Discussion

4.5.1. Foraging associations

In common with most mammalian carnivores, the honey badger is solitary and has not been recorded to hunt cooperatively with con-specifics, except on occasion as mother-cub pairs (Chapter 2). Yet the honey badger is observed to forage in association with individuals of seven other species (two mammals, five birds) in the KTP. Since the ant-eating chat predominantly catches insects that are disturbed while the honey badger is digging for vertebrate prey, this relationship appears to be one of commensalism, which has been reported in a wide variety of birds and mammals (Dean & Macdonald, 1981).

The relationships between the honey badger, chanting-goshawk and jackal (and possibly the three owl species and African wild cat) are more complicated as associating individuals appear to catch the prey items that the honey badger is digging for. As these are generally small mammals and small reptiles, only the successful hunter can feed and there is no potential for food sharing (Packer & Ruttan, 1988).

There is little doubt that the associating individuals benefit directly from the digging efforts of honey badgers. In chanting-goshawks in particular, the strike rate and strike success appear to be substantially higher when they are hunting with a honey badger than when hunting alone or in conspecific groups in a similar habitat for similar prey (Malan & Crowe, 1996). The association also extends the prey base of the exclusively diurnal goshawk to include nocturnal prey species that are normally unavailable to it when it hunts alone (i.e. *P. garrulous, T. brantsii, G. paeba;* Malan & Crowe, 1996). Foraging with a honey badger may increase the reproductive and survival fitness of chanting-goshawks, particularly since they have been observed to take food back to the nest after foraging with a honey badger. This association may be particularly common in an open habitat that offers excellent visibility for the associating species.

No data is available on the hunting success and hunting rate of the black-backed jackal when hunting alone in similar habitat and thus no direct comparisons could be made. While many species show rigidity in their foraging strategies (Bouskila, 1998), the jackal switched from its typical active hunting strategy (Ferguson, 1980) to a "sit-and-wait" strategy when foraging with the honey badger, and this is likely to decrease the handling and search costs for the jackal. In addition, the association is likely to provide increased opportunities for the jackal to catch prey above ground. Ferguson (1980) suggests that when jackals hunt alone, mice and small reptiles frequently escape into holes in the ground and are thereafter unavailable to a jackal, as in only one case was a jackal successful at digging them out. An investigation into a similar foraging association between the coyote *Canis latrans* and American badger *Taxidea taxus* when hunting squirrels showed that the association benefited the coyote with an increased consumption rate (Minta *et al.*, 1992), but possible benefits to the American badger were unclear.

Current theory suggests that mutualism is best viewed as reciprocal exploitations that nonetheless provide net benefits to each partner rather than as reciprocal beneficial relationships (Herre *et al.*, 1999). It has been shown that the associating individuals benefit from the association by exploiting the prey that escape while a honey badger is digging, but there is little evidence to suggest that a honey badger benefits in terms of increased capture success and intake rate or decreased search time through cooperative hunting. While honey badgers are aware of associating individuals and react to their behaviour, this seldom results in their own successful capture of a prey item. Unlike the foraging association between the yellow billed hornbill and dwarf mongoose (Rasa, 1983), there is also no evidence that either chanting-goshawks or the jackals warn honey badgers of potential predators.

Many interactions between animals can usefully be regarded as a ‘producer / scrounger” relationships where one species of individual (scrounger) uses the behavioural investment of another (producer) to obtain a limited resource (Barnard & Sibley, 1981). Scroungers reduce the costs of exploiting the resource (in this case, food) by letting the producers invest the necessary time and energy in foraging and then usurping the results of their efforts. Producers can maximize their food intake by staying far away from potential scroungers, who in turn can maximize their intake by staying near potential producers (Flynn & Giraldeau, 1998; Giraldeau & Mottley, 1998). In the large carnivores, kleptoparasitism or food stealing is fairly common and usually involves one carnivore scavenging prey from the other (Creel *et al.*, 2001). In this study, the associating species (“scroungers”) always initiated the interaction, and both jackals and goshawks were observed to wait at a resting burrow for a honey badger to emerge. However, honey badgers did not appear to avoid the associating species (i.e. by going into a hole, or shifting their activity schedule) and were rarely aggressive towards the associating individuals.

Compared to the kleptoparasitism in large carnivores where group of females or subadult lions might lose almost 20 % (Cooper, 1991), and cheetahs, 9.2 % (Caro, 1994), of the edible portion of their kills to spotted hyaena, honey badgers lose less than 5 % of their overall potential prey to jackals and only 2 % to goshawks. As a result of the low hunting success of honey badgers when chasing prey items above ground, the majority of prey items that escaped during digging events are unavailable to honey badgers even when associating individuals are not present.

The data show that both jackals and chanting-goshawks were more commonly seen with female honey badgers than males. This may be due to the lower hunting success of females and the higher number of prey that escape during digging events. Since female honey badgers spend 90 % of their active time foraging while males are also frequently engaged in non foraging activities i.e. scent marking, long distance trotting and male-male interactions (Chapter 3), females may be more productive for associating species to follow. In addition, jackals and chanting-goshawks may be more likely to randomly encounter foraging females than males.

It is considered unlikely that the small decrease in intake by a honey badger during an association, results in a decrease in the overall fitness of the honey badger, and these associations are most likely to be an example of facultative commensalism. However, both jackals and chanting-goshawks appear to most frequently follow honey badgers in the cold-dry season, which is the "lean" season for the honey badger in the KTP (Chapter 2), and this may also be the "lean" season for the jackal and chanting-goshawk since they take similar prey. It is during this season that the associations are likely to have the greatest negative effect on the honey badger, particularly the jackal / honey badger association.

Both the chanting-goshawk and jackal frequently hunt with con-specifics and are likely to benefit from social learning i.e. learn from con-specifics, and this may facilitate the spread of the association within a population. Sasvari & Hegyi (1999) have shown that tits are able to learn that they can successfully find food near heterospecifics from con-specifics and thereafter followed the heterospecific individual during the next bout of foraging. These associations are likely to be reinforced by regular interactions and are likely to be sensitive to anthropogenic disturbance. For instance, persecution outside of protected areas may result in the honey badger adopting exclusively nocturnal habits (pers. obs.), and this will result in a decoupling of its association with the goshawk. Berger (1999) suggests that a desensitization in interspecific responsiveness can occur in less than ten generations.

Anecdotal observations of the dark chanting-goshawk *Melierax metabates* and jackal following the honey badger in more wooded, mesic habitats in the lowveld of South Africa (I. Thomas, pers. comm.; P. Chadwick pers. comm.) and the observation that Ethiopian wolves were observed to follow honey badgers in the Bale mountains of Ethiopia (Sillero-Zubiri, 1996), suggests that these interspecific foraging associations may be widespread, and simply more commonly seen in open habitats. Similar opportunistic hunting associations have also been observed between the pale chanting-goshawk and slender mongoose *Galerella sanguinea* (Dean & Macdonald, 1981), black-footed cat *Felis lybica* and marsh owl *Asio capensis* (Sliwa, 1994), pied kingfisher *Ceryle rudis* and Cape clawless otter *Aonyx capensis* (Boschoff, 1978) and the African marsh harrier *Circus ranivorus* and grey mongoose *Galerella pulverulenta* (Lombard, 1989). It is likely that these are also facultative commensalism and the result of opportunistic predators keying in to the opportunities provided by the hunting efforts of other species.

4.5.2 Aggressive interactions

In the KTP, the majority of aggressive interspecific interactions between the honey badger and other species were asymmetrical (one species the aggressor; Palomares & Caro, 1999) and could largely be predicted by relative body size. All small carnivores weighing < 1 kg are prey of the honey badger, as are the young of medium sized carnivores (bat-eared fox, Cape fox, African wild cat and probably aardwolf and black-backed jackal) that are in the same size class. The interaction between the honey badger and the jackal appears to be symmetrical (both species kill each other's young) with aggression initiated by both species. A honey badger has been recorded to kill jackal pups in a den in Etosha, Namibia (Hancock, 1999) and Dragesco-Joffe (1993) reports of two golden jackals *Canis aureus* killing a honey badger in northern Niger. The interactions between the honey badger and other medium sized carnivores commonly involved direct biting, and this may have important consequences for the spread of diseases. The honey badger is known to be a carrier of rabies (Bingham *et al.*, 1997) and has been associated with outbreaks of rabies amongst black-backed jackals (Bingham, pers. comm.). A honey badger faecal sample from the Kalahari also indicated infection with feline panleukopenia virus, a sub group of feline parvovirus (Steinel *et al.*, 2000), and canine distemper has also been implicated in honey badger deaths (McKenzie, 1993; Kingdon, 1989; L. Hunter, pers. comm..).

There appears to be a large amount of dietary overlap between medium-sized mammalian carnivores, with murids the predominant prey items (honey badger: Chapter 2; African wild cat: Skinner & Smithers, 1990; black-backed jackal: Ferguson, 1980; Nel, 1984; Cape fox: Nel, 1984), medium sized raptors (Steyn, 1982) and large snakes (Sprawl & Branch, 1995). While it is probable that differences in hunting behaviour and habitat and prey selection reduce the ecological overlap between these species (Simberloff & Dayan, 1991), indirect exploitative competition for food may be an important regulatory factor for these predators (including honey badgers) in the KTP. Certainly, the dietary overlap suggests that the predation of individuals of these species by the honey badger can be termed intraguild predation, which is defined as the killing and eating of species that use similar, potentially limiting resources and are therefore potential competitors (Polis & McCormick, 1987; Holt & Polis, 1997). A record of a honey badger dragging a small cheetah cub in the Kruger National Park (M. Allsopp, pers. comm.) suggests that the honey badger may also kill the young of the larger predators, but this could not be confirmed.

Despite its reputation as invincible with no natural enemies (Skinnner & Smithers, 1990), the honey badger is preyed on by leopard, lion and possibly spotted hyaena in the KTP. In addition there are several accounts of honey badgers killed by leopard (Turnbull-Kemp, 1967; Bailey, 1993), lion (Pienaar, 1969), spotted hyaneas (Pienaar *et al.*, 1987) and wild dog (Pienaar *et al.*, 1987) from other areas. Brown hyaena and cheetah appeared to be cautious of confrontation with the honey badger, and Mills (1990) and Owens & Owens (1978) report brown hyaenas initially chasing honey badgers but aborting the attack in the face of the honey badger's threat display. The predation of honey badgers by large predators lessens the likelihood that the long hair on cheetah cubs serves to protect them (the cheetah cubs) from large mammalian predators as lion and spotted hyaena are also major predators of cheetah cubs (Laurenson, 1995). However, the mimicry may be intended for aerial predators and no records of aerial predators killing a honey badger could be found. The honey badger appears to be particularly vulnerable to predation as it is frequently unaware of its surroundings when digging, is easily surprised and is a relatively slow runner (Appendix A; pers. obs). To offset this, it generally avoids contact with the large mammalian carnivores, and when it is surprised at close quarters, it utilizes a formidable and frequently successful threat display to dissuade potential predators.

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- Chapter 5 -

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

5.1 Abstract

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

5.2 Introduction

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

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

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

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

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

5.3 Study area and methods

5.3.1 Study Area

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

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

5.3.2 Data collection

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

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

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

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

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

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

5.3.2 Data analysis

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

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

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

5.4 Results

5.4.1 Home range

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

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

Table 5.1 Home range size of female and male (young & adult) honey badgers in the KTP, showing the periods of observations, and number of points. Home range area is calculated as the 100 % & 95 % MCP of all points and the 100 % MCP from only burrow positions, where sufficient points are available.

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

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

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

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

Figure 5.1 Incremental area analysis of two habituated male honey badgers showing the change in the range area as successive burrow positions were collected. Am 4 home range size = 640 km ^{2}, n =104 resting positions; Am12 home range size = 625 km ^{2}; n = 107 resting positions.

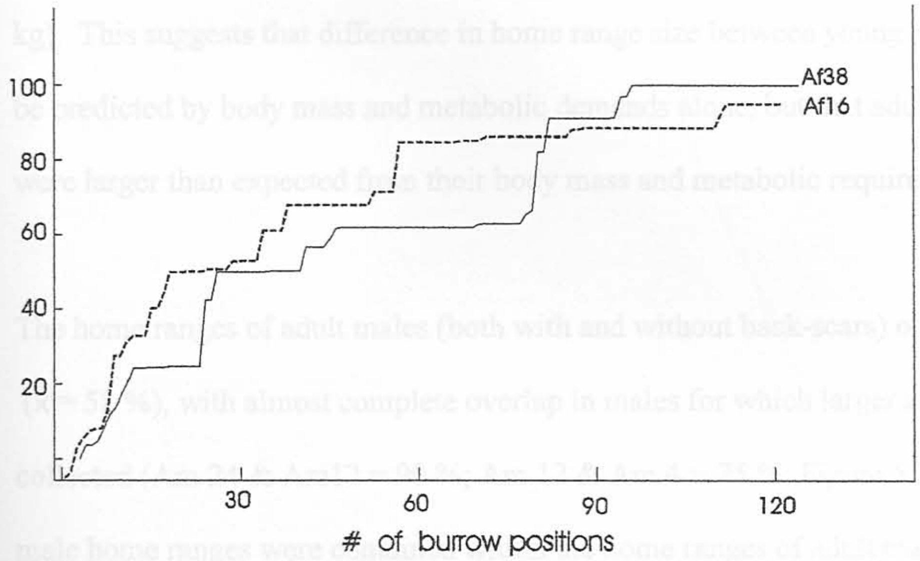


Figure 5.2 Incremental area analysis of two habituated female honey badgers showing the change in the range area as successive burrow positions were collected. Am38 home range size = 81 km^2, n = 124 resting positions; Af16 home range size = 167 km^2; n = 123 resting positions.

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

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

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

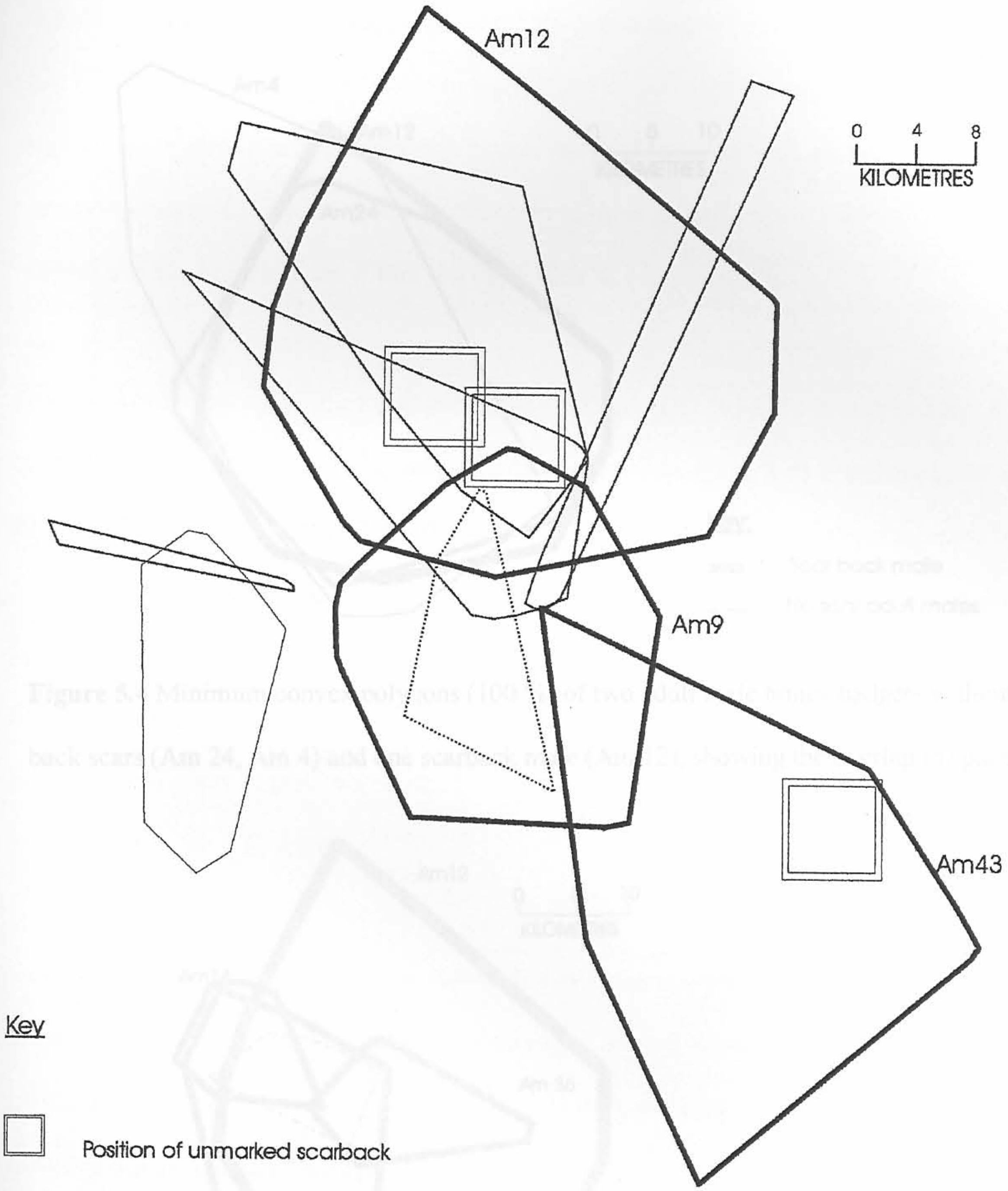


Figure 5.3 Minimum convex polygons (100 %) of nine radio-marked scar-back male honey badgers and the spot positions of three unmarked, scarback males. More than 30 locations were available for the three individuals shown in bold (Am12, Am 43, Am 9), with less than 30 positions for the other six individuals.

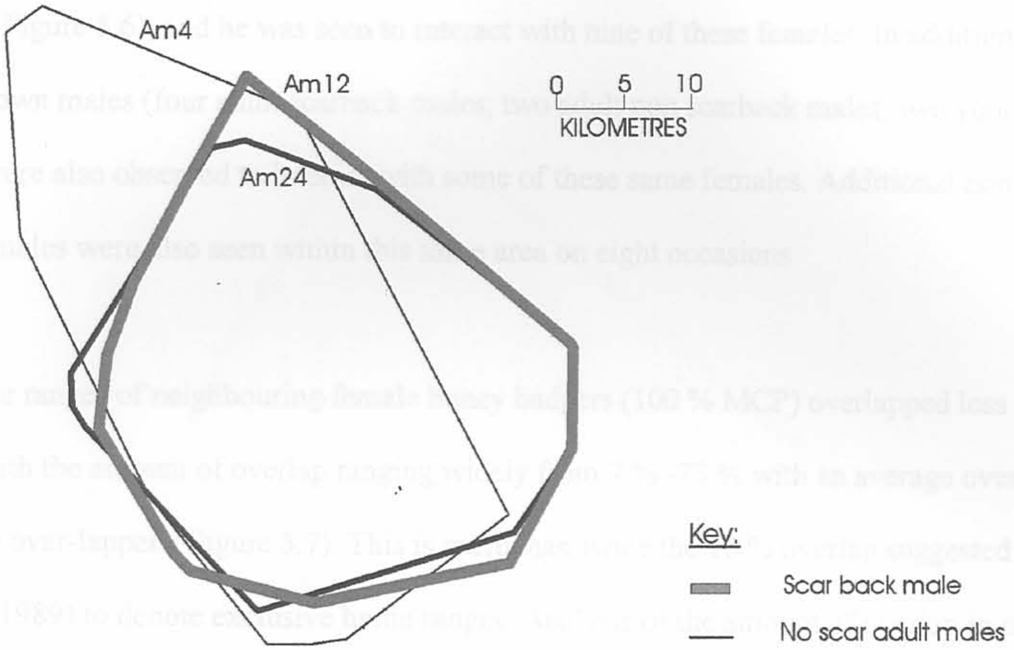


Figure 5.4 Minimum convex polygons (100 %) of two adult male honey badgers without back scars (Am 24, Am 4) and one scarback male (Am 12), showing the overlap in space use.

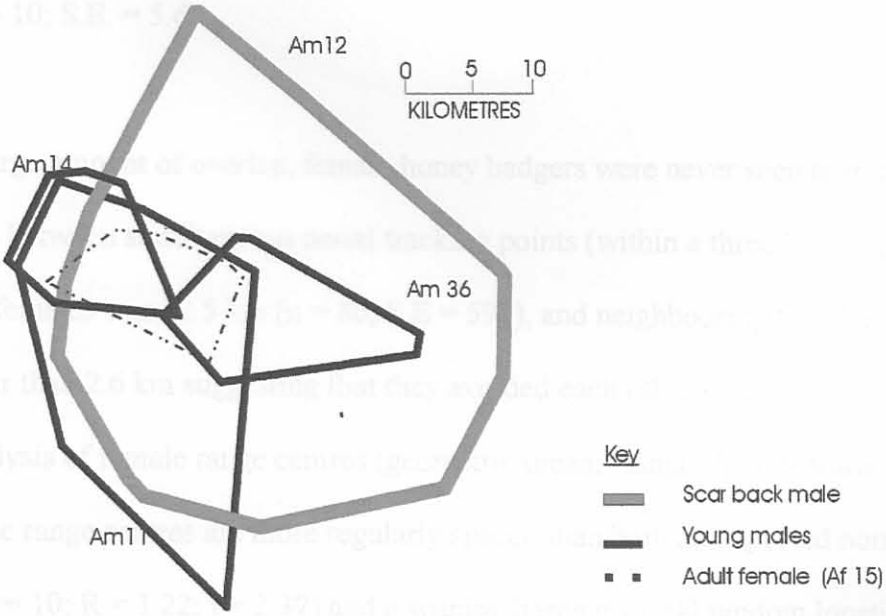


Figure 5.5 Minimum convex polygons (100 %) enclosing all positions of three young males (Am 11, Am3 6, Am 14) and one adult scarback male (Am 12). The natal home range of Am14 when he was still dependent on his mother (Af15) is also shown by the dotted line.

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

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

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

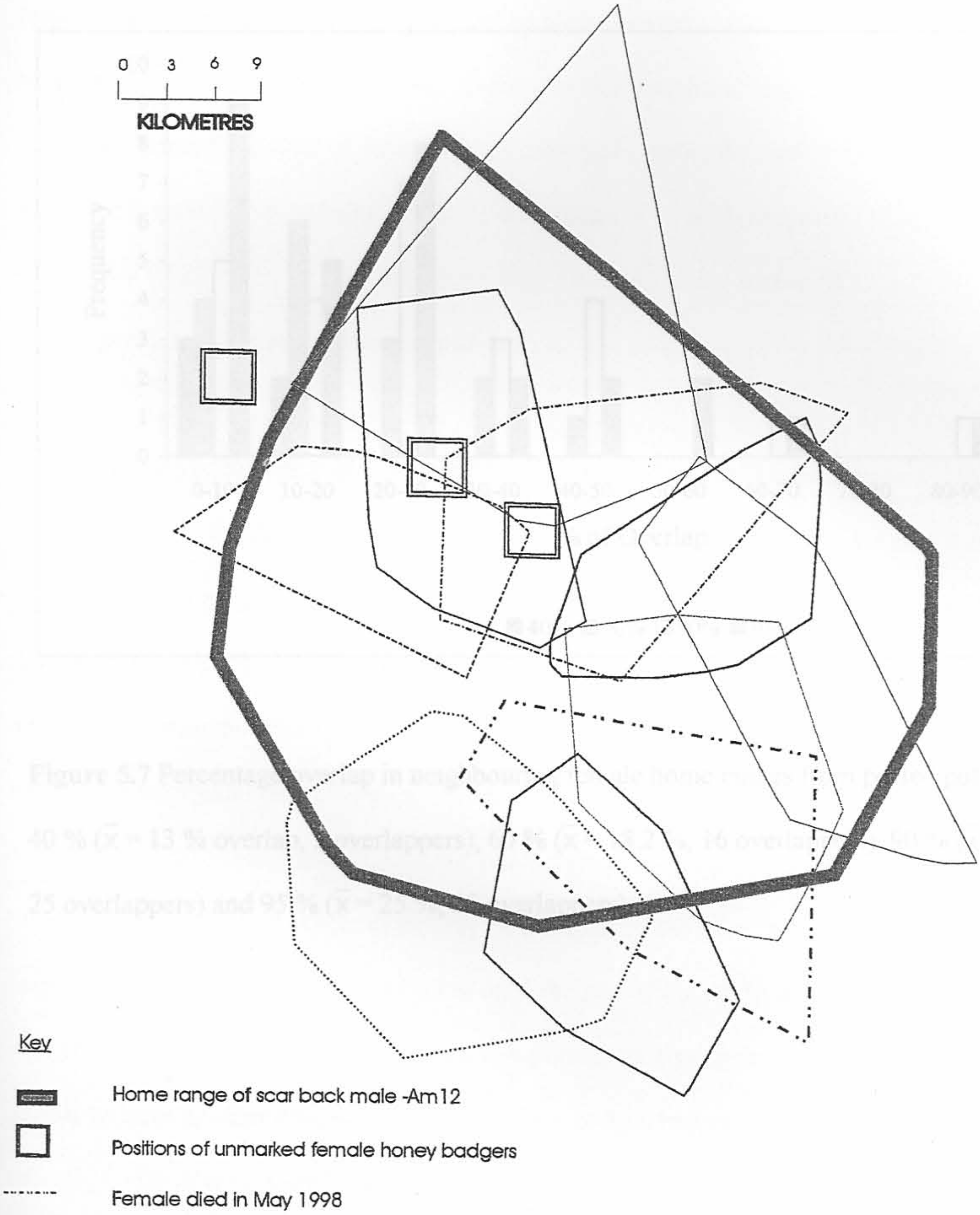


Figure 5.6 Home range outlines (100 % minimum convex polygons of all points) of ten radio-marked female honey badgers showing the range overlap and size of female home ranges in relation to an adult scarback male honey badger (Am12) utilizing the same area. The positions of three unmarked females within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

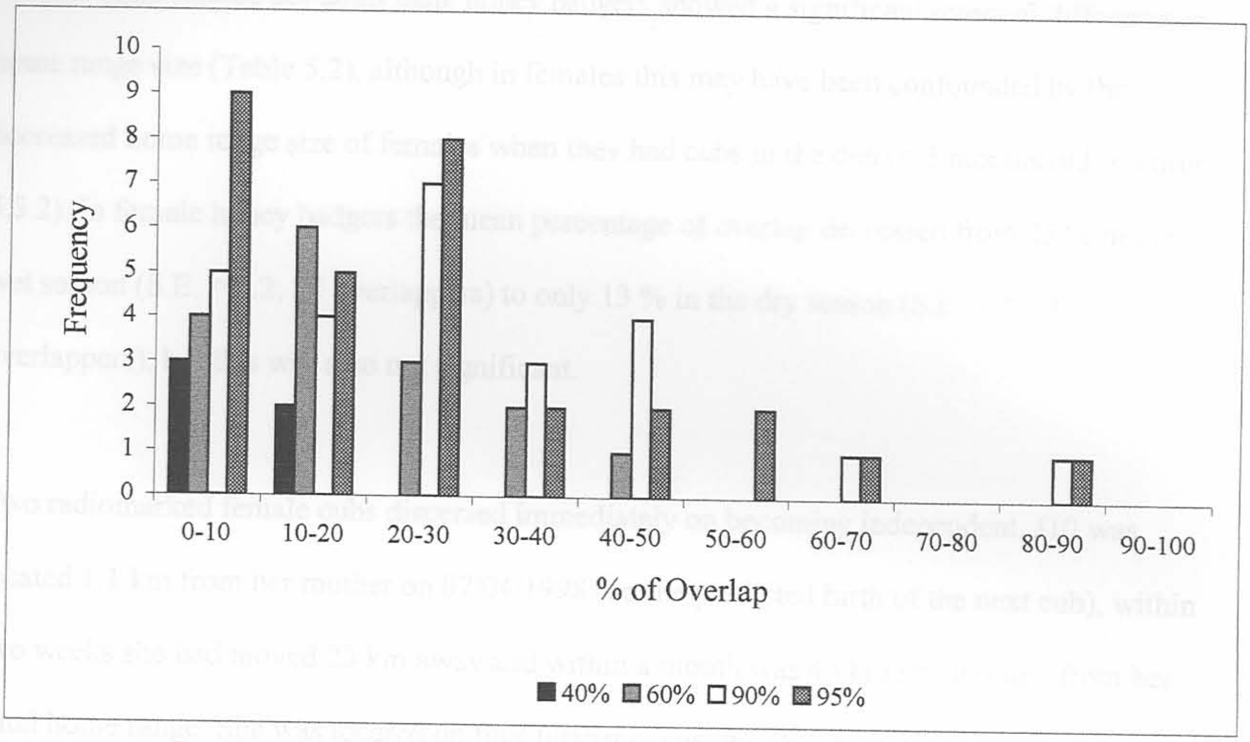


Figure 5.7 Percentage overlap in neighbouring female home ranges from peeled polygons of 40 % ($\bar{x}$ = 13 % overlap, 5 overlappers), 60 % ($\bar{x}$ = 18.2 %, 16 overlappers), 90 % ($\bar{x}$ = 28 %, 25 overlappers) and 95 % ($\bar{x}$ = 25 %, 30 overlappers).

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

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

Table 5.2 Comparison of the dry (May – Aug) and wet season (Sep - Apr) home ranges in male and females honey badgers in the KTP. Home ranges were calculated as the 100 % MCP from resting positions for individuals where at least 30 locations were available for each season. In females, the home ranges of individuals with cubs in the den (< 3 months old) are marked in bold (section 5.4.2).

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

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

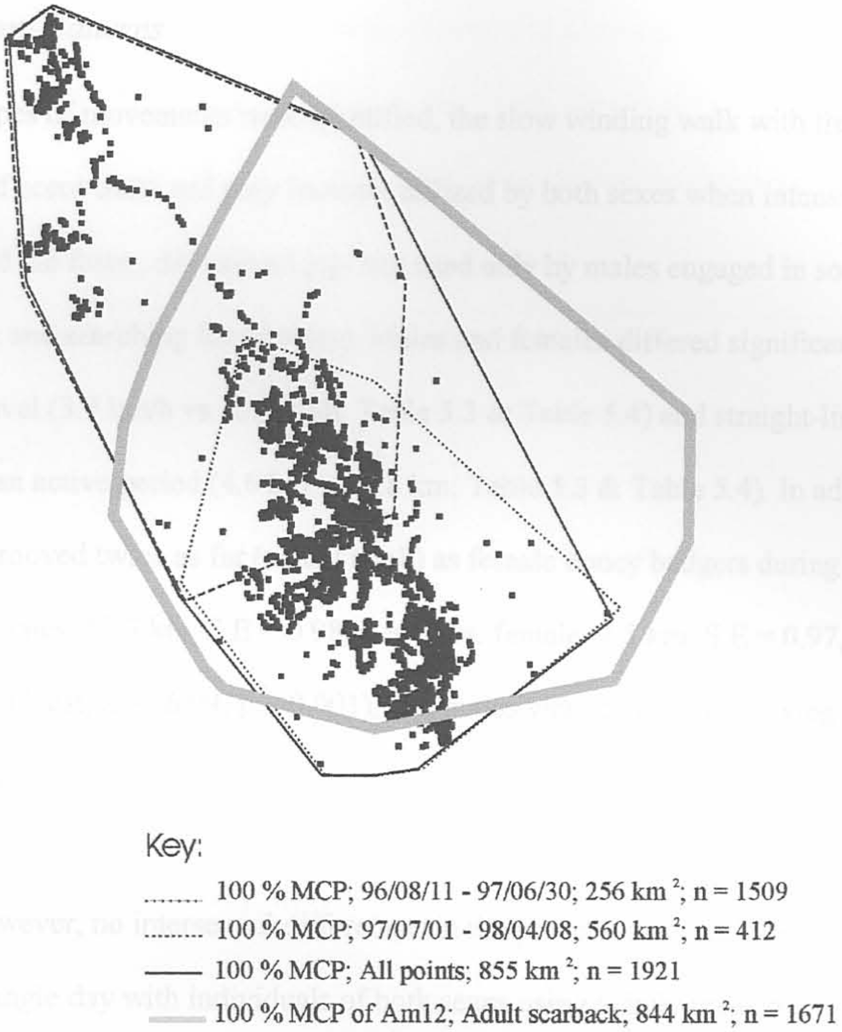


Figure 5.8 Increase in the size of a young male's home range over a 20 month period (100 % MCP of all points; Am 4), showing the initial relatively small home range for 11 months followed by a rapid expansion and shift in home range area. The home range of an adult scarback male (Am12; dominant male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

5.4.2 Movement Patterns

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

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

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

Table 5.3 The median rate of travel, distance moved and percentage of home range used each day in male and female honey badgers. The median (with sample sizes in brackets) rather than the mean is presented as the data have a skewed distribution and were analysed with a Mann-Whitney U test.

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

Table 5.4 Comparison of rate of travel, straight line distances and percentage of home range used per day in different age and sex categories. In all cases Mann-Whitney tests were used.

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

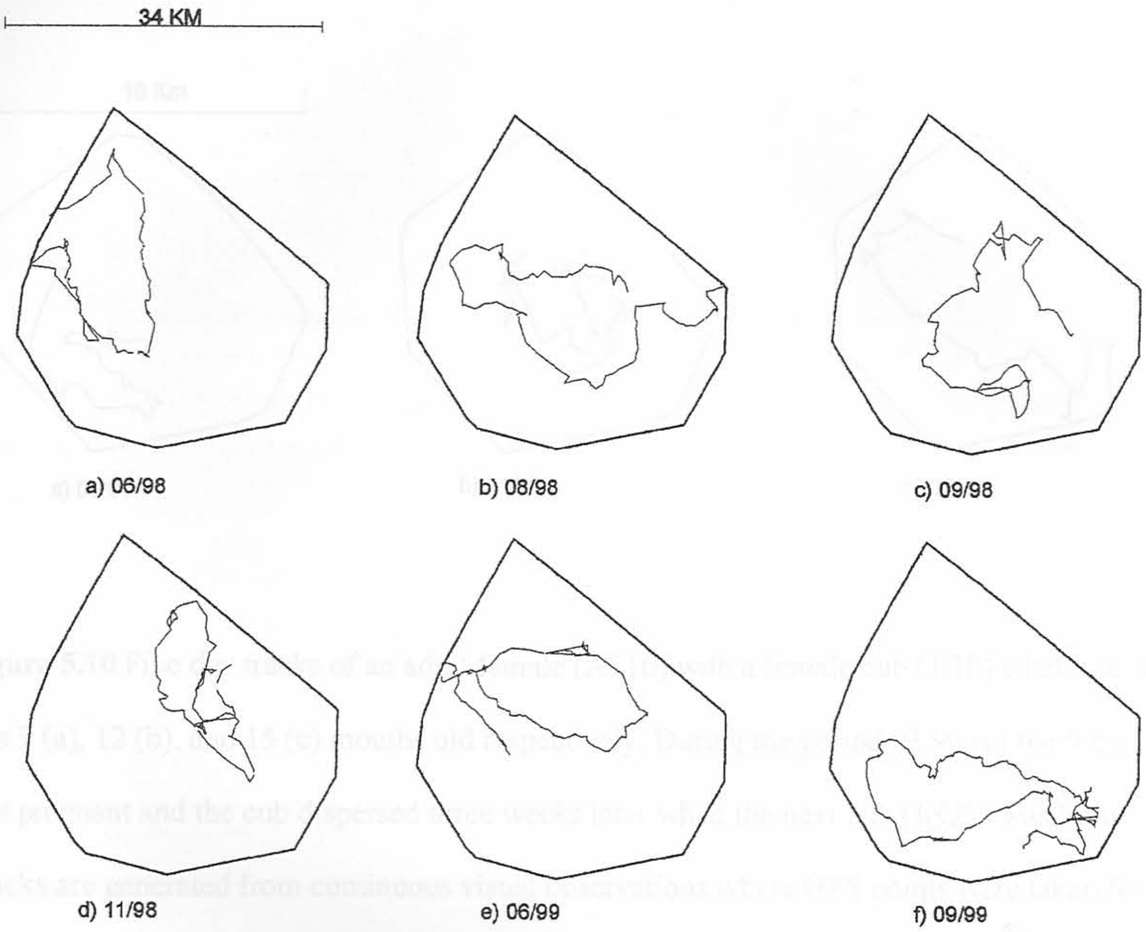
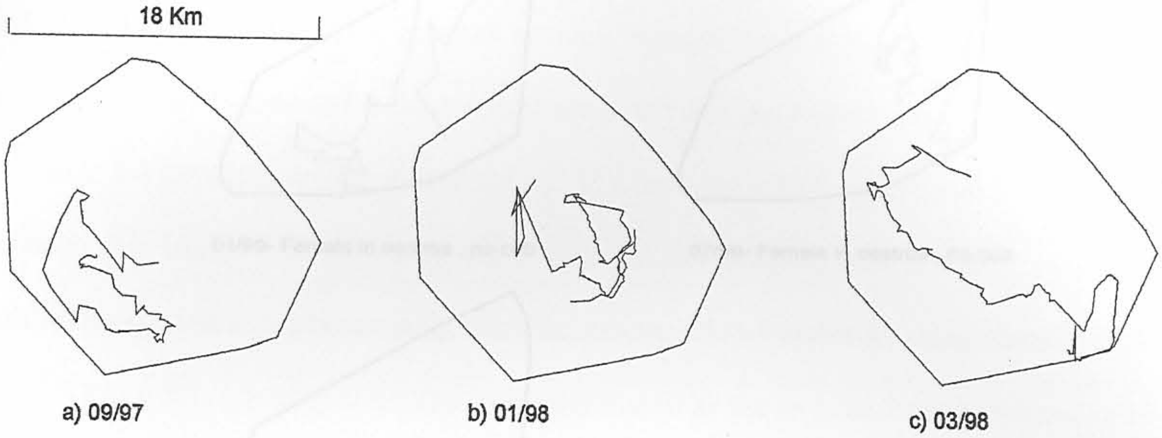
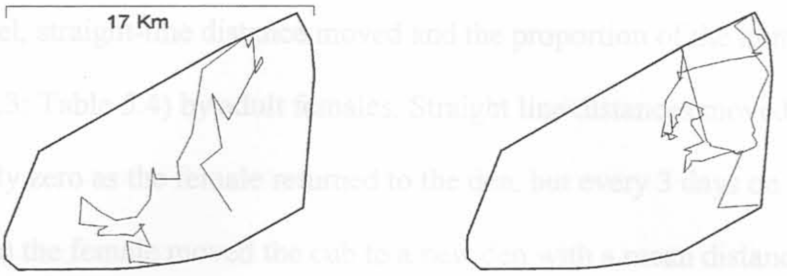


Figure 5.9 Five day tracks of an adult male scar-back honey badger (Am12) during different months of the year, over a 15 month period.

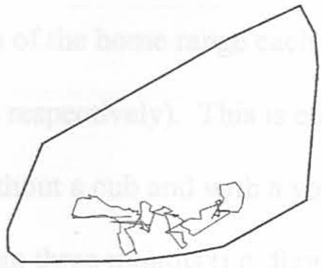


a) 09/97 b) 01/98 c) 03/98

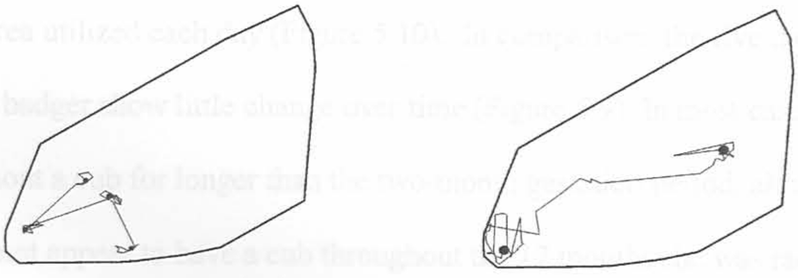
Figure 5.10 Five day tracks of an adult female (Af 16) with a female cub (Jf10) when the cub was 9 (a), 12 (b), and 15 (c) months old respectively. During the period 03/98 (c) the female was pregnant and the cub dispersed three weeks later when the next cub (J♂27) was born. Tracks are generated from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



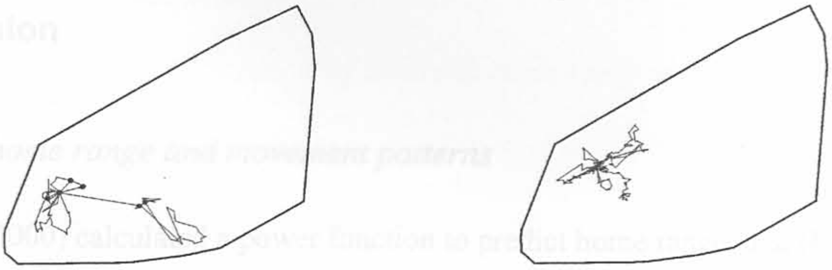
01/99- Female in oestrus , no cub 07/99- Female in oestrus , no cub



09/99- Female pregnant, no cub



03/99- Female with one month old cub 10/99- Female with one month old cub



05/99- Female with two month old cub 06 /99- Female with three month old cub

Figure 5.11 Five-day tracks of an adult female during oestrus and pregnancy (no cub) and with den cubs of different ages within her home range, where black dots represent den sites. No data were available for this female with a foraging cub (>3 months old). Tracks are generated from continuous visual observations where GPS points were taken for each change in behaviour or at 10-minute intervals.

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

5.5. Discussion

5.5.1 Female home range and movement patterns

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

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

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

Figure 5.12 Comparison of the average home range area in nine medium sized mustelids (> 5 kg), showing the relatively large home range of the honey badger and the wolverine *Gulo gulo.* All data except for the honey badger from Johnson *et al.* (2000) with the following scientific names: American badger *Taxidea taxus,* European river otter *Lutra lutra*; North American river otter *Lontra canadensis*; Indian smooth coated otter *Lutrogale perspicillata*; European badger *Meles meles*; sea otter *Enhydra lutris* and giant otter *Pteronura brasiliensis.*

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

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

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

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

5.5.2 Male home ranges and movement patterns

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

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

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

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

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

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

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

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

5.6 References

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- Chapter 6 -

Scent marking behaviour of the honey badger *Mellivora capensis* (Mustelidae) in the southern Kalahari.

6.1. Abstract

Data from direct observations of habituated individuals and spoor tracking are used to investigate sexual and seasonal patterns in the scent marking behaviour of the honey badger *Mellivora capensis*. Four categories of scent marking are identified; scent marking at latrines, token urination in holes along the foraging path, squat marking and anal drag at single use sites and functional excretion. No seasonal differences in scent marking behaviour were recorded in either males or females. In adult males, 79 % of scent marking behaviour occurs at latrines and the use of latrines appears to be related to advertising social status and maintaining the dominance hierarchy through "scent matching". Female latrine visits were relatively rare and related to advertising reproductive status and possibly assessing potential mates. Token urination was used extensively in females and young males, and its association with foraging behaviour and successful digging events suggests that urine may mediate spatio-temporal separation and/or resource utilization. In common with other mustelids, scent marking is an important form of communication in the honey badger and this study provides direct observations of the behavioural contexts in which scent marking occurs.

6.2 Introduction

Even solitary animals must have an effective communication system to maintain their social organisation and ensure reproductive success. Chemical or olfactory communication enables solitary animals to leave messages that are relatively long lasting, can be "read" later by conspecifics, and can also be used at night, under ground or in dense vegetation (Clapperton, 1989; Hutchings & White, 2000). As a result almost all carnivores scent mark by depositing urine, faeces and /or other glandular secretions onto features in the environment (Macdonald, 1980).

In addition to marking with token amounts of faeces and urine (Macdonald, 1985), several mustelid species deposit faeces at communal latrines, which are thought to play a role in territorial maintenance and as information sites for other members of the population (Kruuk, 1978; Roper *et al.,* 1993; Stewart *et al.,* 1997). All mustelids also possess paired anal scent glands, which act as reservoirs for secretions from tubular and sebaceous glands (Gorman & Trowbridge, 1989). The use of anal gland secretions has been described in a variety of mustelid species including the ferret *Mustela furo* (Clapperton, 1989), stoat *M. erminea* (Erlinge *et al.,* 1982), mink *M. vison* (Dunstone, 1993), polecat *M. putorius (*Lode, 1994*),* European badger *Meles meles* (Kruuk *et al.,* 1984), wolverine *Gulo gulo* (Koehler *et al.,* 1980), and European otter *Lutra lutra,* (Kruuk, 1995). Marking with subcaudal, chin, foot and ventral glands (Erlinge *et al.,* 1982; Macdonald, 1985) and through scratching and rolling (Macdonald, 1980) has also been recorded.

The function of scent marking has been widely debated over the last two decades (reviews by Gosling, 1982; Macdonald, 1985; Gorman & Trowbridge, 1989) and is most often associated with advertising the occupation and ownership of a territory (Gosling, 1982; Gorman *et al.,* 1984; Clapperton *et al.*, 1988; Richardson, 1991). Alternative suggestions are that scent marking is related to the maintenance of dominance hierarchies (Gosling, 1982; Gosling *et al.*, 1996), reproduction and the detection of oestrus (Ewer, 1973; Macdonald, 1985; Gorman & Trowbridge, 1989), interactions between predators and prey (Viitala *et al.*, 1995), foraging (Macdonald, 1980; Kruuk, 1995), mediation of the spatio-temporal separation of neighbours ("railway signals"; Clapperton, 1989), group membership (Gorman & Trowbridge, 1989) and the orientation of an individual within its own range (Lyall-Watson, 1964 in Gosling, 1982).

In this chapter, results are presented from the first study of scent marking behaviour in the honey badger *Mellivora capensis*, a solitary mustelid. While no previous information on the scent marking behaviour of the honey badger in the wild is available, anecdotal accounts report frequent anal gland "squat marking" by honey badgers kept as pets (Sikes, 1964). Pocock (1920) noted that the honey badger's anal pouch was unusual among mustelids in being reversible, as it is in some mongooses and hyaenas (Kingdon, 1989). In addition, the honey badger has enlarged anal glands in common with members of the subfamilies *Galictis, Ictonyx, Mephitis and Conepatus,* and it produces a foul- smelling evacuate into the air when in danger and is therefore considered aposematic (Macdonald, 1985).

The honey badger provides a particularly interesting case study as it does not follow the typical mustelid spacing pattern of intrasexual territoriality (Powell, 1979; Chapter 5), and it is a non-seasonal breeder in the Kalahari (Chapter 7). Adult males have large (548 km^2) home ranges that overlap extensively if not completely with other males and encompass the smaller home ranges of young males (187 km^2) and several females (138 km^2; Chapter 5). There is evidence of a dominance hierarchy between adult males and groups of 2-5 individuals travel together on occasion (Chapter 7). In contrast, female home ranges show an average overlap of

25 %, but females avoid each other temporally, and adult females have never been seen to interact (Chapter 7).

In this chapter, the repertoire of scent marking behaviours and patterns of scent-marking in space and time in the honey badger are described for the first time. Direct observations of free-living honey badgers allowed scent-marking events to be described in the environmental and behavioural contexts in which they occurred. The results are then compared to predictions from hypotheses on the function of scent marking (Table 6.1).

6.3 Study area and methods

The study was initiated in July 1996 and continued until December 1999 (42 months) in the Kgalagadi Transfrontier Park (KTP), which encompasses an area of 36 200 km^2 with the Kalahari Gemsbok National Park, South Africa (KGNP)and neighbouring Gemsbok National Park, Botswana. It is a semi desert region and the vegetation is described by Acocks (1988) as the western form of Kalahari Thornveld with a very open savanna of *Acacia haemotoxylon* and *Acacia erioloba* with desert grasses. This study was primarily conducted in the central dune area of the KGNP, which is characterized by medium to high dunes on reddish sands where *A. haemotoxlon* appears in a shrub-like form with occasional *Boscia albitrunca* and *A. erioloba* trees. Dune areas are interspersed with slightly undulating open plains areas, with similar plant composition but with no *B. albitrunca* trees, and pans and yellowish sands, which support shrub veld of *Rhigozum tricophorum* and *Monechma sp.* (Van Rooyen *et al.*, 2001).

6.3.1. Data collection

Details of capture, radio marking and habituation are presented in detail in Appendix A. All captured honey badgers were divided into four age categories based on tooth wear, age and body size: den cubs (< 3 months.); foraging cubs (still dependent on adult females; 3 -16 months), young adults (1 - 3 yrs) and adults (> 3 years). In males, young adults and adults were clearly separated on the basis of testes size and mass although they showed no differences in linear dimensions (Chapter 7). Adult males were further divided into males with a prominent back scar and those without a back scar, with the assumption that scarback males were older than non scarback males as there is some evidence that the scar develops over time (Chapter 7). The back scar is a raised area or callus in the middle of the back thought to be caused by repeated intraspecific biting in the same area over time (Chapter 7). Since young females dispersed out of the study area at independence (> 50 km from natal home range), it was not possible to assess young female scent-marking behaviour.

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Twenty-five individuals (13 females and 12 males) were radio marked with Telonics radio-collars. Nine radio-marked adult badgers (five females with five cubs and four males) were habituated to the vehicle until they could be followed without any obvious influence on their behaviour. Habituation also allowed observation of non-habituated individuals during interactions, as the non-habituated individual seemed to take their cue from the habituated individuals and frequently relaxed in our presence. Additional information was provided by spot observations of radio marked individuals and spoor tracking by a Khomani San tracker.

Direct observations (5811 hours) were used to determine the behaviour and frequency of scent marking behaviour, and observation periods 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 minutes to 20 hours. During all observations honey badgers were observed from the roof of a vehicle 10-30 m away depending on visibility and grass height. All activities were timed and described, and where possible interactions between individuals were filmed (16 mm) and photographed for closer examination. In all cases the GPS position, position of scent mark in the environment, behaviour before and after scent marking, and general description of scent marking behaviour were noted.

Latrines (common defaecation sites containing signs of at least two visits) could only be located by following (visual or spoor tracking) honey badgers and were thus always active on first identification. They were assigned individual consecutive numbers and their GPS position and a basic description of size, shape, habitat, and prominent landmarks were noted. A sample of latrines (11 in 1997 but increased to 24 in 1998, and 46 in 1999) was visited at the beginning of each month for three years to assess changes in use over time. Signs of activity i.e. spoor, scats, urine were noted, and all recent scats deposited within that month were counted and removed. A latrine was considered active if one or more fresh scats were found during a monthly check.

6.3.2. *Data analysis*

Quantitative data on the rates of scent marking were calculated as scent marking events per hour of activity per individual, and compared seasonally and in different age and sex groups using non-parametric Kruskal-Wallis and Mann-Whitney U-tests with post-hoc non parametric multiple comparison testing (Q-test; Zar, 1999). Chi-square tests were used to test for differences in the frequency of use of different types of scent marking while ANOVA was used to test for differences in the mean duration of latrine visits. The positions of latrines and scent marking sites were plotted using GPS coordinates imported into RANGES V: An analysis system for biological location data (Kenward, 1991).

6.3.3. Hypotheses related to scent marking in non territorial carnivores

Of the many hypotheses proposed for the function of scent marking, several are not considered here as they do not apply to the honey badger, lack clear predictions or cannot be tested in the field (see Gorman & Trowbridge, 1989). These included suggestions that scent marks assist in pair bond formation (Rothman & Mech, 1979), provide information on group membership (Gorman & Trowbridge, 1989), deter and/or intimidate intruders (Hediger, 1949; Geist, 1965; Richardson, 1991), provide the marker with self assurance and a sense of ownership (Mykytowycz, 1975), or assist in population regulation (Gosling, 1982). The six hypotheses and predictions addressed in this study are outlined in Table 6.1.

6.4. Results

6.4.1. Types of scent marking

Six types of scent marking behaviour were identified in honey badgers:

a) **Anal drag:** The honey badger assumes a squatting position with the pelvis depressed so that the anus touches the ground, and "walks" forward with the forelegs, moving in a straight line (< 0.5 m) or in circles. The tail is raised in an arc over the back of the body. The anus is dragged along the substrate (sand, grass tuft, tree root or log), and secretions from the anal gland are thought to be deposited as has been shown in other mustelids (Clapperton *et al.*, 1988; Kruuk, 1995). The anal drag is frequently accompanied by intensive smelling of the ground and urine may also be dribbled.

b) **Squatmarking**: Similar to the anal drag, the animal assumes a squatting position and briefly presses the anus to the ground repeatedly, either in the same place or whilst gradually moving forward, using a bobbing motion. The honey badger may squat mark 1 - 52 times consecutively during this behaviour. Squat marking frequently occurs after a bout of intensive smelling with the nose touching the ground or object

Table 6.1 Main hypotheses and predictions related to the function of scent marking in mustelids.

Hypothesis	Predictions	References
A. Scent–matching / dominance	a) Owners mark the territory to maximize the chance that marks will be detected. b) Owners mark more than subordinates c) Owners mark themselves with substances used to mark area d) Owners make themselves available for scent matching. e) Owners remove or replace marks of others. f) Non owners should withdraw from owner if the scent of the owner matches scent marks encountered in the area.	Gosling, 1982; Ralls, 1971; Gorman *et al.*, 1984
B. Signal reproductive status (females)	a) Intersexual differences in scent marking. b) Change in frequency of marking by females when in oestrus or during breeding season c) Females place marks where males are most likely to encounter marks. d) Males respond to female marks	Clapperton, 1989

Table 6.1 (continued on next page)

Table 6.1 (cont.)

C: Spatio-temporal separation (females)	a) No seasonal changes in rates of scent deposition. b) Marking should increase in areas of overlap. c) Individuals must be able to determine freshness of mark.	Clapperton *et al.*, 1988; Clapperton, 1989
D: Foraging efficiency (males & females)	a) No difference between sexes. b) Marking should occur near foraging areas. c) Marking should occur before, during or after foraging bouts. d) Marking should increase when resources are scarce and resources are patchy but replenishing	Kruuk, 1995

of interest. It is assumed that secretions from the anal glands are deposited during squat marking.

c) **Body-neck rubbing**: The dorsal surface of the belly, neck and chin are rubbed backwards, forwards and side ways on the sand, with the front legs splayed and the tail raised above the body. Body rubbing only occurs in conjunction with other scent marking behaviours and was never seen on its own. It takes places after other scent marking behaviours i.e. anal drag, squat mark, urination and defaecation, in the same area where these behaviours occurred. While it is occasionally followed by more scent marking, it usually leads to vigorous bouts of scratching prior to the end of scent marking activity at that site.

d) **Scratching and rolling:** Intensive periods of scratching are frequently observed during and after intensive scent marking, and Macdonald (1985) suggested that this may release odours.

e) **Token urination:** Small amounts (few drops) of urine are dribbled from a squatting position. This is easily distinguished from functional urination where large amounts of urine are excreted above ground in a single event.

f) **Functional excretion-scats and urine:** Scats are deposited from a squatting position, both in association with other scent marking behaviours at latrines and alone. When deposited in association with other scent marking behaviours scats are always placed above ground (often at common scent marking sites or latrines) but when deposited alone are usually placed in holes along the movement path and are frequently placed outside of refuge burrows or on getting up after a rest.

Overall 1034 scent-marking events were directly observed, and they could be clearly categorized into four groups: scent marking at communal areas or latrines involving a combination of scent marking behaviours (n = 236; 22.8 %), token urination in holes (n = 530; 51.3 %), squat mark/anal drag at single use sites (n = 160; 15.4 %) and defaecation and urination not associated with other scent marking behaviours (n = 108; 10.5 %). The low number of excretion events observed suggests that events were missed due to defaecation in the resting burrows and/or defaecation immediately on leaving a resting burrow. While scats (unaccompanied by other scent marking behaviour) are likely to have some marking function, insufficient data precludes further analysis.

There were significant sexual differences (adult males vs. adult females; $\chi^2 = 557$, df = 2, $p < 0.001$, Table 6.2) and in males, age-related differences (young males vs. adult males, $\chi^2 = 167$, df = 2, $p < 0.001$) in the type of scent marking behaviours observed (Table 6.2). Token urination was the most frequent scent marking behaviour observed in adult females and young males, while scent marking at latrines was the most common scent marking activity observed in adult males.

Honey badgers were also observed to release a strong smelling evacuate (yellow liquid) from the anal gland on four occasions when threatened by large predators, such as lion *Panthera leo*, leopard *Panthera pardus*, and spotted hyaena *Crocuta crocuta,* and on all occasions when they were captured. No sexual or age related differences in the release of scent were recorded although there were some individual differences in its potency. In all cases the smell was strong but not suffocating and was released in situations of extreme danger. It was associated with defensive behaviour that included a loud "rattling" vocalization, an erect tail, standing tall, charging, and pilo-erection and was considered part of a threat display. The scent was not

Table 6.2 Number and type of scent marking events visually recorded in male and female honey badgers in the KTP (five females; five adult males; two young males).

Age & sex	Type of scent marking behaviour Latrines n[1] (%)	 Squat-mark/anal drag n (%)	 Token urine n (%)
Adult ♀♀ (5 individuals)	31 (5.1 %)	87 (14.4 %)	486 (80.5 %)
Adult ♂♂ (5 individuals)	190 (78.8 %)	51 (21.2 %)	0
Young ♂♂ (2 individuals)	15 (18.5 %)	22 (27.2 %)	44 (54.3 %)

[1] = Refers to the number of latrine visits.

released during intraspecific interactions, or interactions with the brown hyaena *Hyaena brunnea*, black-backed jackal *Canis mesomelas* or Cape fox *Vulpes chama.*

6.4.2. Latrines

6.4.2.1. Latrine descriptions

A latrine was identified as a site with signs (scats, spoor) of at least two independent visits by a honey badger and 122 latrines were identified during the study. They consisted of a patch of ground laid bare by frequent scent marking and scratching activity with 2 - 52 scats deposited above ground on the bare area. They varied in size (2 - 20 m^2; $\bar{x} = 6$ m^2) and shape from long paths of activity (0.5 x 12 m) to circular latrine patches. The largest latrine found consisted of four circular latrine patches joined by eleven paths in amongst *A. mellifera* bushes, however the large size of this latrine was unusual. Honey badgers made specific trips to latrines, heading in a straight line to a specific latrine from as much as 2.8 km away, but no latrines had definite paths leading into them, and honey badgers approached them from all directions. In 15 cases honey badger latrines were found under the same *B. albitrunca* trees as hyaena latrines. They were most commonly found on dune slopes (70.2 %), followed by dune troughs (23.8 %), but seldom on dune crests (6.4 %).

The majority of latrines (59 %) were located beside or under trees, which were prominent visual landmarks in the open Kalahari landscape (at least from a human perspective), with the remainder in the open (28.6 %) or beside *A. mellifera* and *A. haemotoxylon* shrubs (11.7 %; Figure 6.1a). Monthly checks of 69 latrines for at least a year revealed that latrines could be broadly divided into two categories based on their frequency of use. Long-term latrines were active for more than a single season (n = 37; 54 %) while "temporary defaecation sites" (TDS, as in Roper *et al.,* 1996) were active for less than a single season and often for only a few days (n = 32; 46 %).

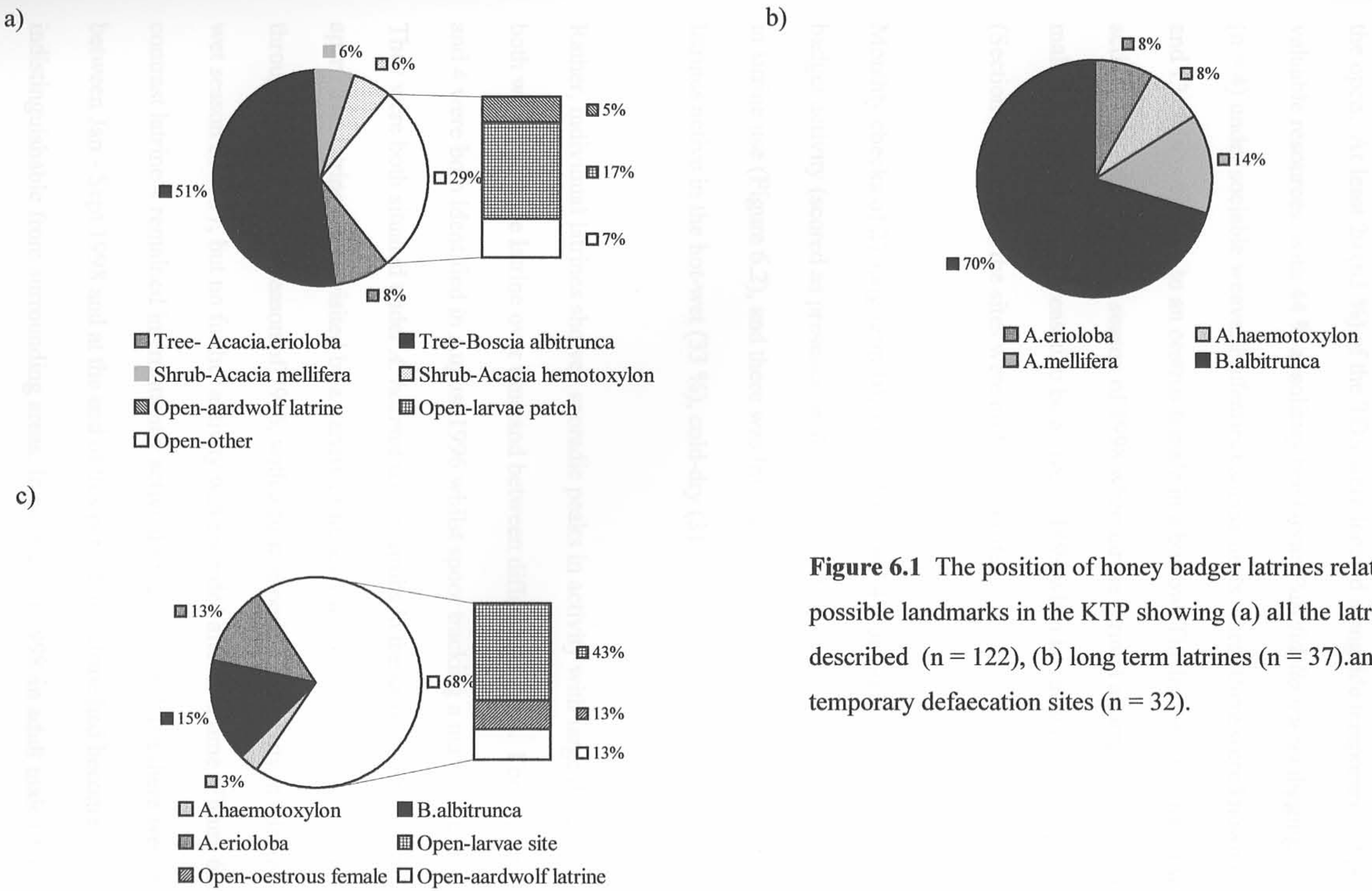

Figure 6.1 The position of honey badger latrines relative to possible landmarks in the KTP showing (a) all the latrines described (n = 122), (b) long term latrines (n = 37).and (c) temporary defaecation sites (n = 32).

The data show that all long-term latrines were located alongside trees (78 %) or shrubs (22 %) and none were found in the open (Figure 6.1b), while in TDS, 68 % (n = 22) were in the open. At least 20 (63 %) of the TDS were located alongside temporary but potentially valuable resources, with 44 % at solitary bee larvae *Parafidelia friesei* digging sites, 13 % (n = 4) under sociable weaver *Philetairus socius* nests where there were known to be chicks and 13 % (n = 4) close to an oestrus female in a burrow. The larvae site latrines were only active during the cold-dry season of 1998 when larvae formed an important part of the diet of male honey badgers and ceased to be active in 1999 when larvae were no longer available (Section 2.4.1.2) and the sites were no longer visited.

Monthly checks of 27 long-term latrines in 1998 and 47 long-term latrines in 1999 for honey badger activity (scored as presence or absence of scats and/or spoor) showed no clear pattern in latrine use (Figure 6.2), and there was little difference in the average percentage of known latrines active in the hot-wet (33 %), cold-dry (31 %) and hot–dry (29 %) seasons of 1999.

Rather, individual latrines showed sporadic peaks in activity with large differences in activity both within a single latrine over time and between different latrines. For example, latrines 1 and 4 were both identified in August 1996 whilst spoor tracking a male honey badger (Am5). They were both situated under *A. haemotoxylon* shrubs in the same habitat and were 2.3 km apart. The latrines were visited by a variety of honey badgers (Am5, Am6, Am4, Af7) throughout the hot-dry season of 1996, with a further period of activity at latrine 1 in the hot-wet season of 1997, but no further activity was recorded after this time (Figure 6.3a). In contrast latrine 4 remained intermittently active throughout 1997, but there were few visits between Jan - Sept 1998 and at the end of this period the latrine had become visually indistinguishable from surrounding areas. In September 1998 an adult male (Am12) visited the latrine and it continued to be active until the end of 1999 (end of the study; Figure 6.3b).

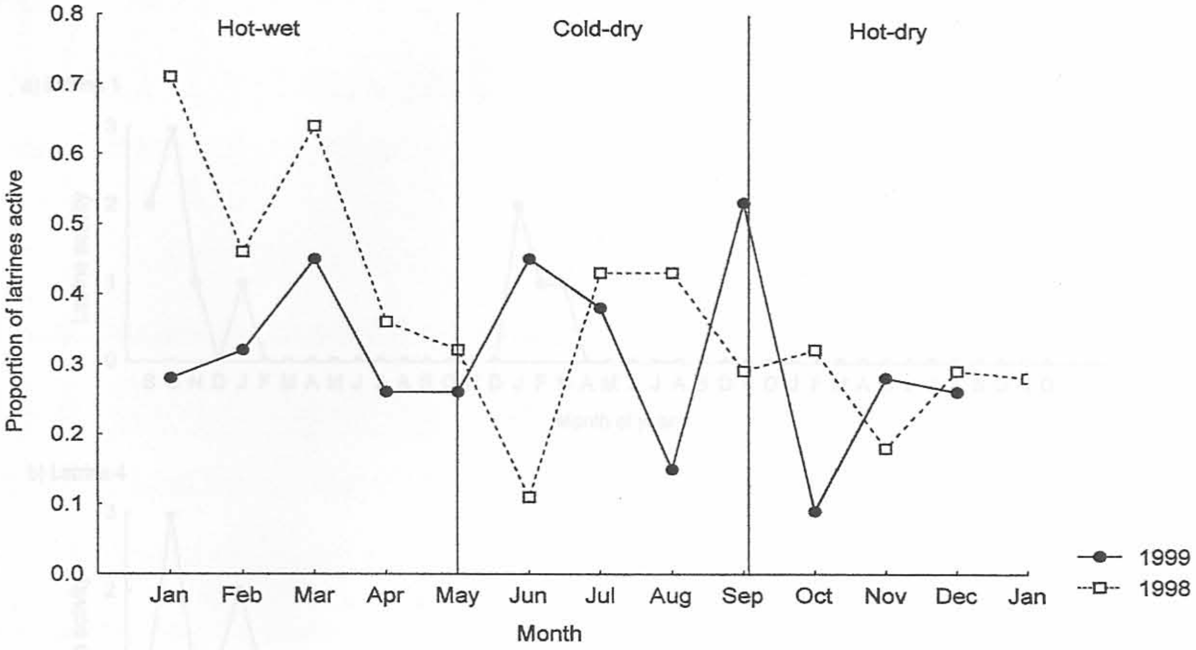

Figure 6.2 Proportion of known honey badger latrines active (scats and/or spoor) during each month of the year for two years in the KTP. Note that there appears to be no seasonal peak in latrine use.

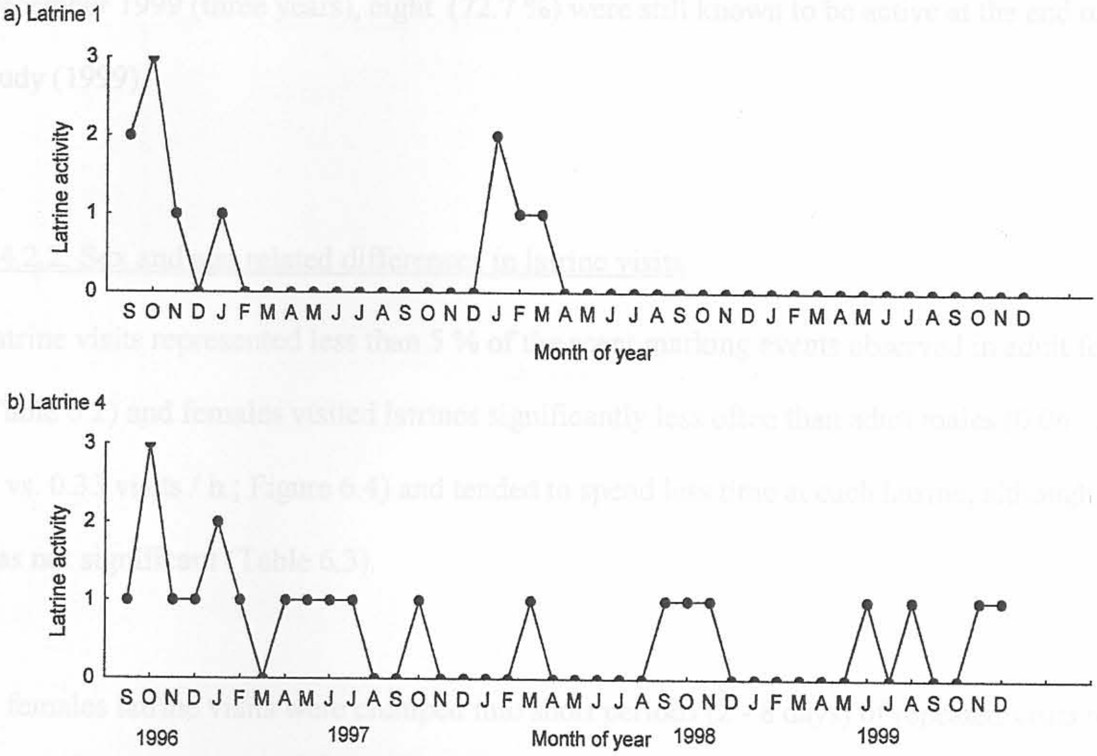

Figure 6.3 Monthly level of activity at two honey badger latrines (1 & 4) for the period September 1996 – December 1999 in the KTP. Note the variation in latrine activity both within and between the two latrines. Activity was scored from 0-3 based on the number of visits in that month where 3 = ≥10 visits, 2 = 5 - 9 visits, 1 = < 5 visits and 0 = no visits.

Of the 11 latrines identified in the hot-dry season of 1996 and checked each month until December 1999 (three years), eight (72.7 %) were still known to be active at the end of the study (1999).

6.4.2.2. Sex and age related differences in latrine visits

Latrine visits represented less than 5 % of the scent marking events observed in adult females (Table 6.2) and females visited latrines significantly less often than adult males (0.06 visits / h. vs. 0.33 visits / h.; Figure 6.4) and tended to spend less time at each latrine, although this was not significant (Table 6.3).

In females latrine visits were clumped into short periods (2 - 8 days) of repeated visits to 2 - 5 latrines separated by up to 14 months of no latrine visits (Figure 6.5). This was not simply a reflection of when a female was followed, as there were long periods of observation when no latrine visits were observed (Figure 6.5). Eight females were observed to visit latrines, and on three occasions, two different females visited the same latrine but at separate times.

Scent marking occurred on only 55 % of female latrine visits and consisted of 1- 4 squat marks in the bare area of the latrine, with a scat and urine left on only one occasion (Table 6.3). Intensive smelling and a slow walk across the entire latrine with the tail erect characterized all female latrine visits (Table 6.3). Females were never seen to belly rub or anal drag either on latrines or elsewhere.

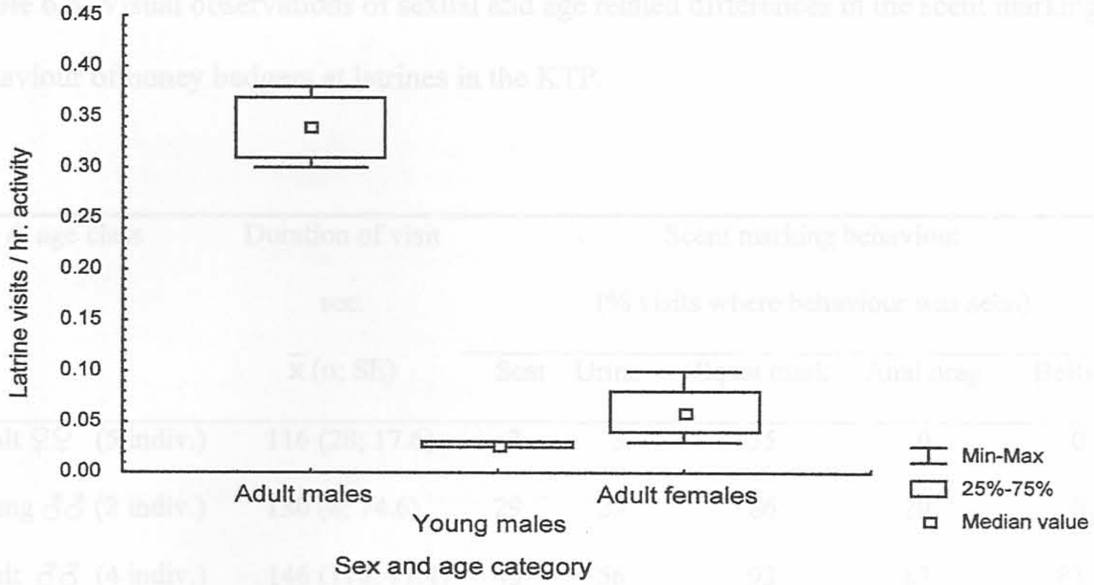

Figure 6.4 The rate of latrine visits in adult female (723 h obs; 5 individuals), adult male (636 h; 4 individuals) and young male (309 h; 2 individuals) honey badgers in the KTP. Kruskal-Wallis test H (2, n = 11) = 8.33; $p < 0.05$ (young males vs. adult males, Q = 2.96, $p < 0.05$; females vs. adult males Q = 2.43, $p < 0.05$; females vs. young males, not significant; Zar, 1999).

Table 6.3 Visual observations of sexual and age related differences in the scent marking behaviour of honey badgers at latrines in the KTP.

Sex & age class	Duration of visit sec. x̄ (n; SE)	Scent marking behaviour (% visits where behaviour was seen)				
		Scat	Urine	Squat mark	Anal drag	Belly rub
Adult ♀♀ (5 indiv.)	116 (28; 17.6)	3	3	55	0	0
Young ♂♂ (2 indiv.)	130 (8; 74.6)	29	29	86	29	0
Adult ♂♂ (4 indiv.)	146 (110; 11.4)	43	56	93	83	83

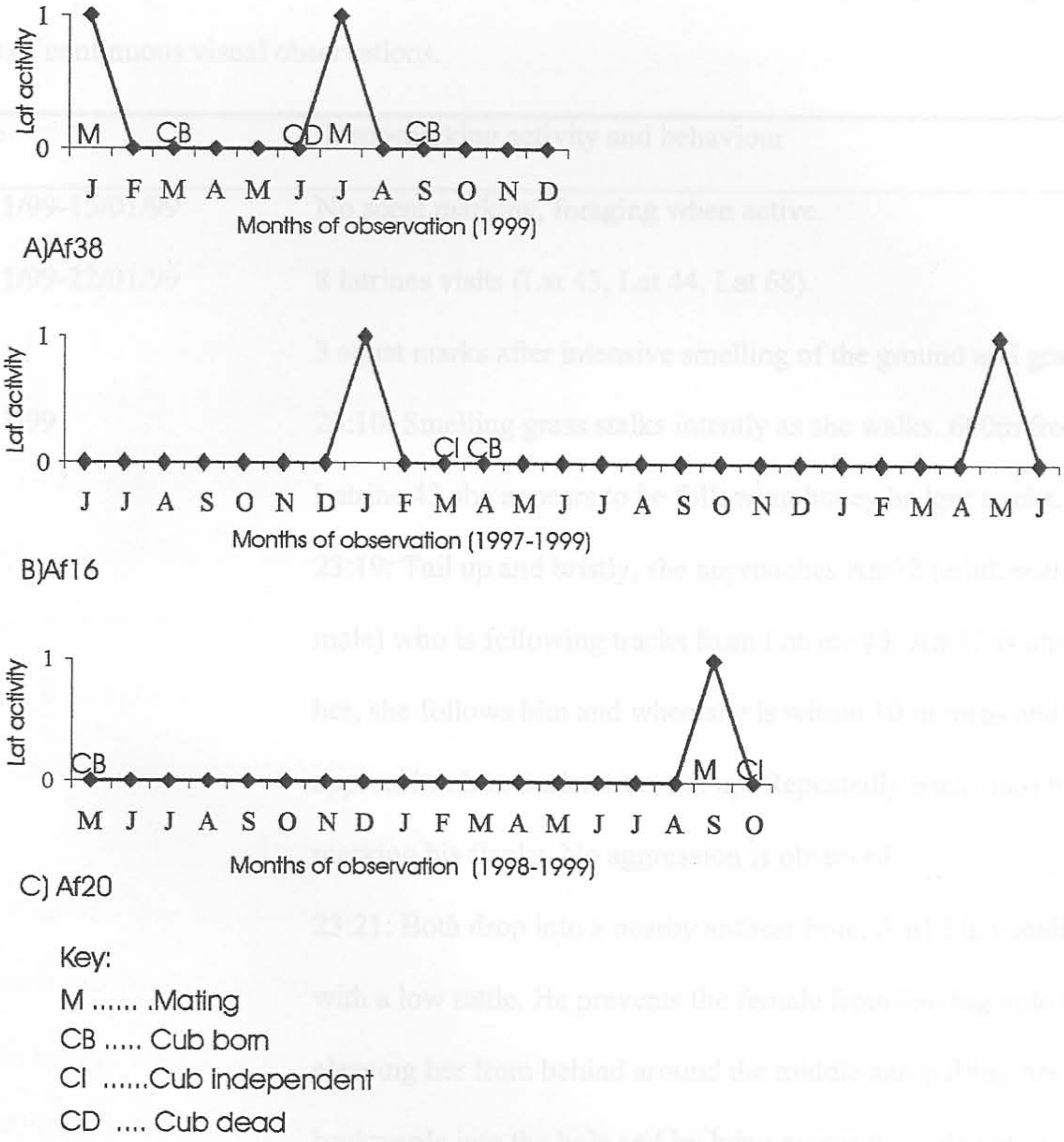

Figure 6.5 The timing of visits to latrines in three habituated female honey badgers over their individual periods of direct observation. Observations of mating, birth of cubs and cub independence are shown to illustrate the association between female latrine visits and reproductive behaviour.

Table 6.4 Scent marking and mating activities of an adult female honey badger during 16 days of continuous visual observations.

Date	Scent-marking activity and behaviour
12/01/99-15/01/99	No scent marking, foraging when active.
16/01/99-22/01/99	8 latrines visits (Lat 43, Lat 44, Lat 68). 3 squat marks after intensive smelling of the ground and grass.
23/01/99	23:10: Smelling grass stalks intently as she walks. 600m from Latrine 43 she appears to be following honey badger tracks. 23:19: Tail up and bristly, she approaches Am12 (adult scarback male) who is following tracks from Latrine 43. Am12 is unaware of her, she follows him and when she is within 10 m turns and approaches him backwards, tail up. Repeatedly backs into him, marking his flanks. No aggression is observed. 23:21: Both drop into a nearby antbear hole, Am12 is vocalising with a low rattle. He prevents the female from leaving hole by clasping her from behind around the middle and pulling her backwards into the hole and by lying across the hole entrance.
23/01/99-26/01/99	Neither honey badger left the mating burrow.
26/01/99	19:19: Am12 left the burrow. 20:52: Af38 left the burrow, and started foraging.
27/01/99	No latrine visits or scent marking activity were observed in the female.
20-25/03/99	Cub was born.

Investigation of the timing of these visits suggests that they were used by females to find or assess males for mating (Figure 6.5; Table 6.4). On seven occasions latrine visits culminated in sexual interactions (courtship and mating), on two occasions latrine visits coincided with the dispersal of a full grown cub and on five occasions a new cub was born within two months of known latrine visits (Table 6.4).

In adult male honey badgers, 79 % of their scent marking behaviour occurred at latrines compared to only 19 % in young males (Table 6.2). In addition, adult males visited latrines more frequently than young males (Figure 6.4; 0.33 visits / hr. active vs. 0.03 visits / hr. active). The latrine scent marking behaviour of young males was markedly simpler and less intense than the elaborate scent marking behaviour observed in adult males (Table 6.3). In young males scent marking at latrines consisted primarily of squat marking (86 %) with occasional anal drags, urination and defaecation (Table 6.3). In common with females, the belly/neck rub was not observed (Table 6.3). In contrast, latrine visits by adult males were characterized by elaborate sequences of scent marking behaviour involving squat marking, anal dragging, belly and neck rubbing, scratching and the deposition of scats and urine (Table 6.3). During scent marking the bare sand as well as logs, tree roots, and grass tufts within the latrine area were marked, the penis was erect and urine was frequently dribbled during the squat mark and anal drag. Males deposited scats on latrines on 42 % of their latrine visits and these provided long-term signs of latrine use.

Latrine visits by adult males varied widely in duration from brief visits (< 1 minute) with limited scent marking (squat marking and/or defecation) and cursory smelling to intensive, longer visits (max. 10 min.) where the male repeatedly scent marked over the entire latrine area using the full repertoire of scent marking behaviours described (Section 6.4.1). On 20 % of latrine visits, adult males vocalized while scent marking using a low rattle/grunt also heard during male-male interactions (Chapter 7). On six latrine visits (3 %) adult males were seen to exhibit flehmen where their lips were pulled back in a grimace and the ground or grass was licked. This was also observed on a further 13 occasions (25 %) in association with single squat marking events (i.e. not at latrines), and on six of these events fresh spoor of other honey badgers was seen at the scent marking site. By directly following scent and tracks from latrines, adult males were observed to meet up with females on three occasions and with other adult males on nine occasions.

On 11 occasions groups of 2 - 5 males (Chapter 7) were seen at a latrine at the same time, and four of these events involved habituated males of different ages, which provided an opportunity to document differences in scent marking behaviour. These observations suggest that the dominance hierarchy within adult males (Chapter 7) affects the position of scent marking events on the latrine. On all occasions when a scarback male was observed at a latrine with a non-scarback adult male (n = 4, section 6.3.1), the scar back prevented the non-scarback and other young males from marking near the center of the latrine by physical "pushing" and intimidation.

On one occasion (26/08/99) three habituated male honey badgers consisting of a young male (Ym 36), an adult male without a back scar (Am 24) and an adult male with a prominent back scar (Am12) were observed at the latrine. Field notes describing the behaviour of the individuals are detailed below.

" <u>26/08/1998 (19:36 - 19:42):</u> *Am24 arrives at latrine 5, Am12 & Ym36 are already present. Am12 is standing tall, hair on end, stiff-legged, tail erect and bottle brushed. He slowly walks up to Am24 and pushes him aside (flanks touching) to the edge of latrine. Am 24 has his head low and backs off, vocalizing with a high pitched, clacking sound while Am12 vocalizes with a low, short, grunt, rattle. Ym36 is ignored by both males but also has his head low and is seen* *to squat mark twice on the edge of latrine area. Am 24 marks on the edge of the latrine, using the anal drag, squat mark, belly rub, scat and urine. At the same time Am12 marks near the center of latrine, also with the anal drag, squat mark, belly rub, scat and urine. Am12 repeatedly prevents Am24 from moving onto the center of the latrine by pushing him sideways until Am24 backs off. All three leave the latrine together in a line (Am24, Am12 then Ym36). Am12 has his tail up, while Ym36 & Am24 have their tails down."*

Latrines appeared to be scattered throughout the home range (hinterland) and were not only located on the boundaries of individual male home ranges (Figure 6.6). This would be expected given the extensive overlap in male range use (Figure 6.6, Chapter 5). Detailed information on latrine use over time and the distribution of latrines within an adult male home range was provided by regular visual observations (1226 h) of a habituated scarback male (Am12) over a two-year period. Of the 69 latrines identified within the home range of Am12, twelve latrines were not seen to be visited by him although they were known to be active during the period of study, and at least 31 (45.6 %) were also utilized by other males. On average four latrines (range 0 - 10) were visited each day, with 50 % of the latrines visited more than once and ten of these latrines visited on more than five occasions (Figure 6.6).

6.4.3. Token urination

Token urination was never observed in adult males, but it was the most common form of scent marking in both females and young males (Table 6.2) although at a significantly lower rate in young males (Figure 6.7).

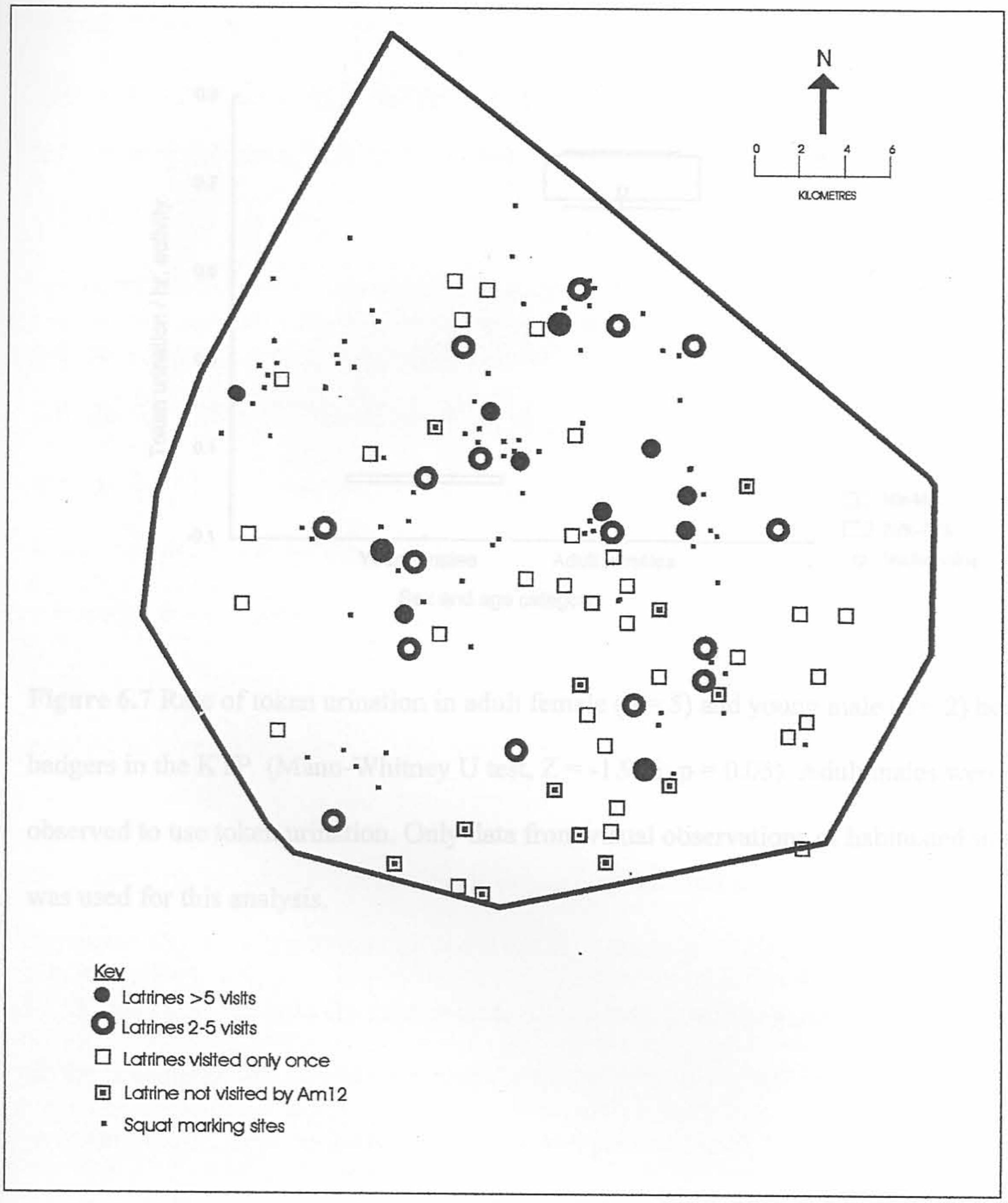

Figure 6.6 Spatial distribution of latrines and scent marking sites within the minimum convex polygon home range outline of an adult male honey badger (Am12). Note the hinterland distribution of latrines and scent marking sites.

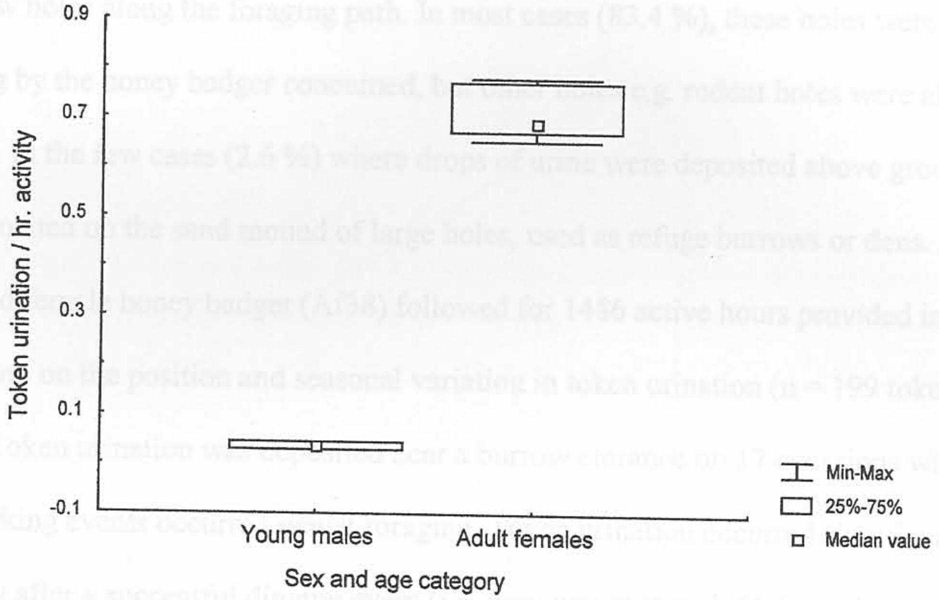

Figure 6.7 Rate of token urination in adult female (n = 5) and young male (n = 2) honey badgers in the KTP (Mann-Whitney U test, Z = -1.936; p = 0.05). Adult males were not observed to use token urination. Only data from visual observations of habituated individuals was used for this analysis.

In both females and young males, drops of urine were commonly (97.4 %, n = 530) deposited in shallow holes along the foraging path. In most cases (83.4 %), these holes were foraging holes dug by the honey badger concerned, but other holes e.g. rodent holes were also used (13.4 %). In the few cases (2.6 %) where drops of urine were deposited above ground, they were deposited on the sand mound of large holes, used as refuge burrows or dens. A habituated female honey badger (Af38) followed for 1486 active hours provided in depth information on the position and seasonal variation in token urination (n = 199 token urination events). Token urination was deposited near a burrow entrance on 17 occasions while 182 scent marking events occurred whilst foraging. Token urination occurred significantly more frequently after a successful digging event (i.e. prey was captured; 66.5 %) than after an unsuccessful digging event (33.5 %; binomial test; $L_1 = 0.426$; $L_2 = 0.579$), but only 34 % of successful digging events (n = 359) were scent marked.

Seasonal differences in the rate of urine deposition were not significant although urine was deposited slightly more frequently in the hot dry season (0.77 / km) than in the hot wet season (0.53 / km) with the cold dry intermediate (0.53 / km). In addition, there were no significant differences in the rate of token urination in this female during different reproductive states i.e. in oestrus (0.62 / km), pregnant (0.58 / km) and cub rearing (0.72 / km).

6.4.4. Squat marking

Single squat marking (not at latrines) was the least predictable of all scent marking activities and was seen at varying rates in different individuals with no significant difference in the rate of squat marking of males (adult and young males) and adult females (Figure 6.9). In all cases, squat marking was accompanied by a 'bottlebrush" tail and intensive smelling and nose dabbing of grass stalks and/or the sand, but it occurred under a wide variety of circumstances (Table 6.6).

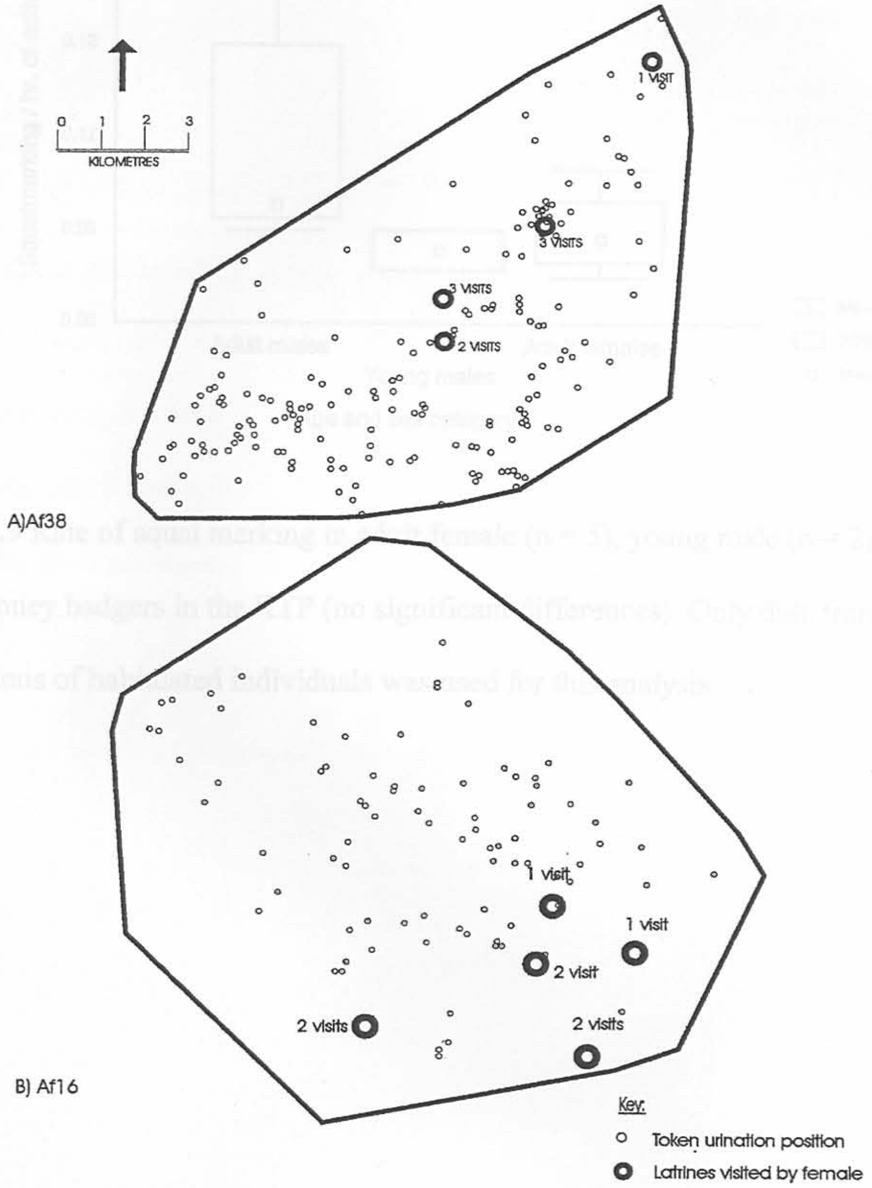

Figure 6.8 Scent marking positions of two adult female honey badgers (Af38, Af16) within their home ranges (105 km^2, 179.7 km^2 respectively). Both the positions of latrines visited by females as well as token urination sites along the foraging paths are indicated.

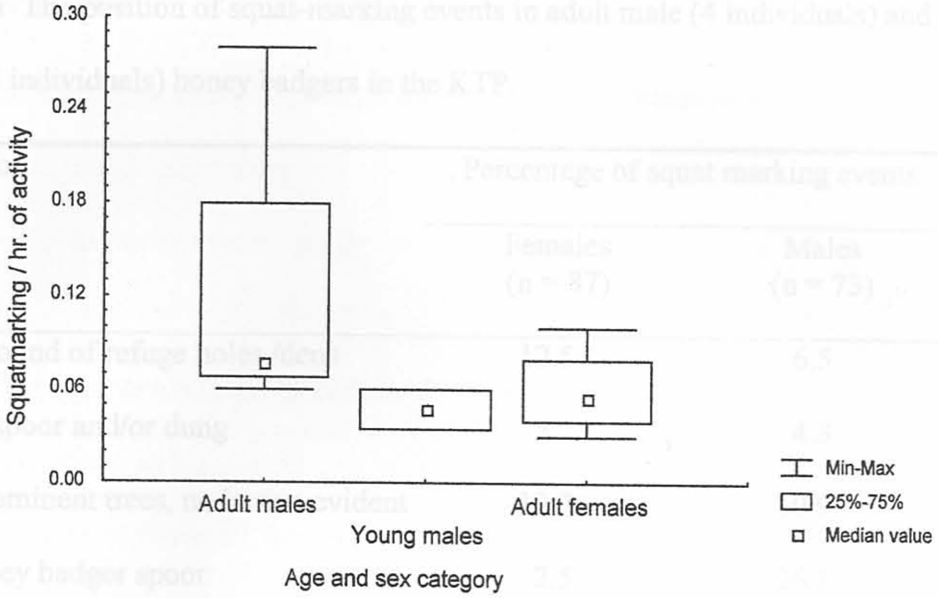

Figure 6.9 Rate of squat marking in adult female (n = 5), young male (n = 2) and adult male (n = 4) honey badgers in the KTP (no significant differences). Only data from visual observations of habituated individuals was used for this analysis.

Table 6.6 The position of squat-marking events in adult male (4 individuals) and adult female (5 individuals) honey badgers in the KTP.

Description	Percentage of squat marking events	
	Females (n = 87)	Males (n = 73)
On the mound of refuge holes /dens	12.5	6.5
Predator spoor and/or dung	5	4.3
Under prominent trees, no latrine evident	13.7	10.9
Fresh honey badger spoor	2.5	26.1
Whitewash under bird nests	0	13.0
In open, no obvious reason.	66.2	39.0

6.5 Discussion

In common with other mustelids, scent marking is an important form of communication in the honey badger, and it uses faeces and urine as well as anal gland secretions to regularly mark objects within its environment. It also releases a potent smelling evacuate from the anal scent gland that is associated with self-defense and threat displays, in common with other mustelids that have enlarged anal glands (Macdonald, 1985). On several occasions honey badgers were observed to break into bee hives, *Apis mellifera* but on no occasion was it observed to use its anal scent glands to fumigate the hives as suggested by Kingdon (1989) and Estes (1991).

Both sexes were seen to scent-mark frequently but in significantly different ways with males predominantly marking at latrines with faeces, urine and anal gland secretions and females predominantly using token urination along the foraging path with some latrine visits. As social odours are a limited resource and in many cases require a significant investment in terms of time and energy, it is predicted that scent marks will be distributed in a way that maximizes their chance of being discovered by the individuals for whom they are intended (Gorman & Trowbridge, 1989). It follows, therefore that scent marks distributed in markedly different ways such as token urination and latrine marking are intended for different recipients and have different functions. The age related differences in male scent marking also suggests that, as in other mammals, scent marking is related to androgen secretion (Ebling, 1977; Fadem & Cole, 1985).

Sexual differences in the type of scent marking has not been widely reported in other mustelids, and Erlinge *et al.* (1982) suggested that marked intersexual differences were a feature of mammals organized into pair or group territories where marking had different functions in the two sexes e.g. the coyote *Canis latrans*. The polygynous honey badger does not fit this description (Chapter 7).

6.5.1. Latrines

Latrine scent marking in males involved the deposition of anal gland secretions (assumed from anal drag and squat marking), faeces and urine, and it proved impossible to assess the function of each type of scent mark independently. Instead a visit to a latrine was considered a single scent marking event, with the deposition of anal gland secretions the primary function of male honey badger latrine visits (93 % of visits). Considering the vastly different chemical compositions of urine, faeces and anal gland secretions (Brinck *et al.*, 1978; Gorman *et al.*, 1978; Erlinge *et al.*, 1982; Davies *et al.*, 1988), it is likely that a variety of messages are being sent and this requires further study.

The use of latrines is not in itself unusual as it has been recorded in many carnivore species, including other mustelids (European badger *M. meles*, European otter *L. lutra*, ferret *M. furo* (Macdonald, 1980; Gorman & Trowbridge, 1989). As in other species, honey badger latrines form conspicuous visual and olfactory landmarks. In most cases it is suggested that latrines have a territorial function where the territories function to defend food resources (Kruuk, 1989) or mates (Roper *et al.*, 1993), but since neither male nor female honey badgers defend a territory (Chapter 5) this hypothesis is not a valid explanation for the latrine scent marking observed.

The significant sexual differences in the rate and scent marking behaviour at latrines, the lack of a seasonal pattern in overall latrine use, the association between female latrine use and reproductive status and between male latrine use and social interactions with both sexes, suggests that latrine use is not related to foraging efficiency (Kruuk, 1995) or spatio-temporal separation (Clapperton, 1989) in either sex, but is rather related to advertising sexual and/or social status.

The "scent matching hypothesis" (Gosling, 1982) was initially developed for territorial animals, but Gosling (1982) suggested that it might be extended to dominance hierarchies. While there is no evidence that dominant individuals produce more or less of a chemical (Gorman & Trowbridge, 1989), there is evidence that marking frequency can reflect the dominance status of marking individuals (Ralls, 1971; Erlinge *et al.*, 1982). Spatial and movement patterns of honey badgers suggest overlap promiscuity (Chapter 5 & 7) with male home ranges overlapping each other as well as a number of females. While male honey badgers are essentially solitary when foraging, groups of 2 - 5 individuals were seen visiting latrines and around females in oestrous (Chapter 8). A dominance hierarchy within males has been described, which seems to determine male access to receptive females (Chapter 7). When the "scent matching hypothesis" (Gosling, 1982; p.94) is directly adapted for use in a non territorial system with a dominance hierarchy, it reads "The function of *non territorial scent marking within a dominance hierarchy* is to provide an olfactory association between *the dominant individual and the marking frequency,* which allows *subordinates* to identify the *dominant individual* when they meet and thus reduce the frequency of escalated agonistic encounters" (my italics for word changes to the original script). The scent marks thus provide a way for a subordinate or a dominant individual to assess the quality of a potential competitor and thus avoid the costs of establishing dominance by overt aggression in every encounter (Kappeler, 1990).

The elaborate scent marking behaviour of males at latrines and subsequent encounters between males provides some support for all six of the predictions of Gosling's (1982) scent matching hypothesis (Table 6.1):

a) *Owner should mark the territory to maximize the chance that marks will be detected.* The observed hinterland distribution of latrines within a male's home range is likely to be the most economical system of marking within such a large area (Mills 1990) as it would maximize the likelihood that a subordinate badger would encounter the scent marks of other individuals (Richardson, 1991; Mills & Gorman, 1987). In common with the brown hyaena *Hyaena brunnea* in the same environment, the majority of long-term honey badger latrines are located under prominent trees e.g. *Boscia albitrunca* in the open landscape, and these may act as visual signposts of the latrine position (Mills, 1990). Shade also retards desiccation and this may prolong the odour value of scent marks. Trees are frequently visited during foraging activities both to look for potential food items (e.g. skinks, rodents, and nesting birds) and for the shade they provide for sand-bathing and resting, and this increases the likelihood of finding a latrine.

b) *Owners (dominants) mark more than subordinates.* It has been shown that subordinates mark less frequently than dominants in most mammals (Ralls, 1971; Gosling, 1982; but see Wenhold & Rasa, 1994). In the honey badger the lower rate of latrine scent marking in young males and the behaviour of subordinates and dominants during combined visits to latrines does suggest that dominant males scent mark more than subordinates. However, further study of honey badgers with larger sample sizes is required to assess whether there is a direct correlation between the rate of scent marking in honey badgers of the same age class but different social ranking. The reason why subordinate males do not increase their marking effort may lie in the costs of marking behaviour i.e. the extra distances to be covered and the amount of lipid secreted (Kruuk *et al.*, 1984).

c) *The owner (dominant) should mark itself with the odour.* Self anointing was not an obvious behaviour in male honey badgers, compared to the behaviour of some ungulates (Gosling, 1982). However, the scratching, rolling and belly / neck rub which occur on a latrine after it has been marked with faeces, urine and anal secretions could serve this function. The belly/neck rub in particular was only seen in adult males and always occurred at the end of a scent marking event in the area on the latrine where scent marking had taken place.

d) *The owner should make himself available for scent matching.* It has been suggested that the scent-matching hypothesis is not appropriate for most solitary carnivore species as encounters between competitors are rare and this prediction is therefore not satisfied (aardwolf *Proteles cristatus*: Richardson, 1991; lion *P. leo*: Funston, 1999). In the honey badger, regular encounters between males may facilitate scent matching (Chapter 7). For instance, adult males were seen to move around in groups of 2 - 5 individuals for up to three days at a time and on occasion actively initiated encounters with other males by following scent found at latrines. The fact that males mark at latrines together, and squat mark along their movement path also provides some evidence that subordinates may be able to match the scent of the dominant with scent marks from a latrine.

e) *The owner should remove or replace marks that do not match his own odour.* Latrines are small, confined areas and since the entire latrine area is marked on a visit it is likely that an individual is marking over the signs of other individuals, although no obvious overmarking behaviour was observed.

f) *Low status individuals should withdraw if the scent of another males matches the smell of the dominant smell found at latrines and higher status individuals should usually withdraw but some encounters should escalate.* This is supported in honey badgers where ritualized agonistic encounters were frequent, but overt aggression was rare and encounters consisted of ritualized intimidation / appeasement behaviour. On the rare occasion that an individual did not retreat or show appeasement behaviour, the encounter escalated into aggressive tumbling, biting and chasing, which reinforced the dominance hierarchy directly (Chapter 7)

The function of latrine visits by females is more difficult to explain. The data suggest that females only visit latrines when they are in oestrus, and since cubs remain dependent on their mothers for long periods (12 – 16 months; Chapter 7) there are long periods between reproductive events. Heightened marking frequency by females around oestrus is common in mammalian carnivores families (Macdonald, 1985), and an obvious explanation for female latrine visits would be to advertise their oestrus state to males to facilitate mating. The observation that males exhibit flehmen at latrines and occasionally find females by following their scent from latrines does suggest that males do indeed find females through latrine visits. However, since females scent marked on less than half of their latrine visits, advertisement of their oestrus state does not seem to be the main function. Instead, female latrine visits were all characterized by intensive smelling of the entire latrine area, which indicates that they may be important sources of information.

Recent studies suggest that females often play a more active role in mate choice than previously suspected (Reynolds, 1996). In the honey badger, more than one male was frequently observed around a single female in oestrus, competing (between themselves) for access to the female. The best strategy for a female is to try to mate with the male that is likely to sire successful offspring. It is possible that just as males assess the dominance ranking of other males through 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.

Visual observations do provide some evidence for female choice as females in oestrus seem reluctant to mate with some males i.e. left the mating burrow at the first opportunity, ran away from the male, or dug out the back end of the burrow and ran off (D & C. Hughes, pers. comm.) 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 (Chapter 7). In the ferret *M. furo*, females do not advertise their oestrus state, and it is suggested that the lack of advertisement is a strategy by females to avoid mating with subordinate males (Clapperton *et al.*, 1988; Clapperton, 1989). This may also be true in the honey badger where a number of males of different status are all looking for females over the same area. Additional research is needed to assess female mate choice further.

Some support for the scent-matching hypothesis in other mustelids has been found in the ferret, which is a solitary mustelid with intrasexual territoriality (Clapperton 1989), as well as in the European badger *M. meles*, which occupies group territories (Kruuk *et al.*, 1984).

Odour is clearly not the only factor used by males or females to assess others as more direct signals such as vocalizations and visual signals such as standing tall and piloerection are also likely to be used in assessment.

6.5.2. Token urination

Urine is known to contain information about reproductive status and oestrus condition (Gorman & Trowbridge, 1989). Since it is the adult female honey badger that predominantly uses token urination, the most likely explanation is that it advertises a female's reproductive status to potential mates. However, the lack of seasonal changes in the rate of token urination, the use of token urination during all stages of a female's reproductive cycle i.e. in oestrus, pregnant and with cubs, the use of token urination in young males and its close association with digging behaviour do not support this hypothesis.

Female honey badgers have large home ranges (138 km^2) that overlap extensively with neighbouring females (Chapter 5). Despite an average home range overlap of 25 %, females were never seen to interact and appear to avoid each other temporally (Chapter 5). Studies on other carnivores have shown that urine can provide temporal information on space use, and animals avoid using areas which have been recently urine marked by conspecifics (Caro, 1994). It is feasible that in the honey badger token urination provides a temporal and historical record of the movements and foraging behaviour of females and young males, and they therefore function as "railway signals" which mediate spatio-temporal separation (Leyhausen & Wolff, 1959; Clapperton, 1989).

A related but not mutually exclusive explanation relates token urination to resource dispersion and "book-keeping" (Henry, 1977; Kruuk, 1995). The small amounts of urine are predominantly placed in holes along the foraging path. If, as predicted, scent marks are distributed in a way that maximizes their chance of being discovered by the intended recipients (Gorman & Trowbridge, 1989), then it is likely that the recipients are intensively foraging honey badgers. Kruuk (1995) suggested that in the European otter *L. lutra* sprainting (marking) behaviour was unrelated to reproductive condition or territory maintenance but was simply used to signal to others where they were feeding and therefore enabled otters to partition resource utilization. Both females and young males frequently move over the same area during consecutive foraging periods (Chapter 6). A temporal and spatial record of where prey items have already been captured might increase foraging efficiency by reducing the amount of time and energy spent foraging in already utilized sites (Henry, 1977; Kruuk, 1995; Clapperton, 1989) and might diminish competition for undisturbed foraging patches (Koehler *et al.*, 1980; Sillero-Zubiri & Macdonald, 1993). In the honey badger this explanation is supported by the increase in token urination in holes were prey was captured, but is complicated by the lack of token urination in adult males.

Adult males have much larger home ranges (548 km^2) than either young males (187 km^2) or females (Chapter 5) and move considerable distances in a 24 h period (Chapter 5). In contrast to females and young male, the limiting resource for adult males is not food, but oestrus females, and as adult males are unlikely to forage over the same area on two consecutive days a system of "book-keeping" might be less important.

6.5.3. Squat marking

The depositing of anal gland secretion through squat marking and anal dragging has been described in a variety of other mustelids and is most commonly associated with territorial behaviour e.g. the European badger *M. meles* (Kruuk *et al.*, 1984), wolverines *Gulo gulo* (Koehler *et al.*, 1980), mink *M. vison* (Brinck *et al.*, 1978) and ferrets *M. furo* (Clapperton, 1989). While no information is available on the chemical composition of anal gland secretions in the honey badger, previous studies on other mustelids have shown that anal gland secretions contain information on individual identity (European badger *M. meles*: Gorman *et al.*, 1984; ferret *M. furo*: Clapperton *et al.*, 1988; stoat *M. erminea*: Erlinge *et al.*, 1982; mink

M. vison: Brinck *et al.*, 1978) and in some cases sexual identity (Clapperton *et al.*, 1988; Erlinge *et al.*, 1982).

In honey badgers, squat marking is the most difficult scent marking activity to explain. It occurs under a variety of conditions and seems primarily to be a response to the odour of potential resources (mates or food) or potential predators. The lack of sexual, seasonal or age related differences in squat marking behaviour and the variety of conditions under which it occurs suggest it is not related to dominance behaviour, reproductive advertisement or foraging efficiency. It may simply be a form of "book-keeping" where places or scents of importance are marked to aid orientation within an individual's home range.

This study emphasizes the importance of direct observations of free-living individuals. While latrines are conspicuous, and visual indications of scent marking behaviour have been relatively well investigated in mustelids, data on the distribution and behaviour of scent marking away from latrine sites are sparse as there are often no long-term signs. In the honey badger, token urination, single use squat marking and the age and sex related differences in latrine marking behaviours would not have been recorded without direct observations and would have lead to an over-simplified account of scent marking behaviour. There is no doubt that direct observation of the behavioural context in which scent marking occurs adds immeasurably to our understanding of its function.

6.6. References

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- 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.

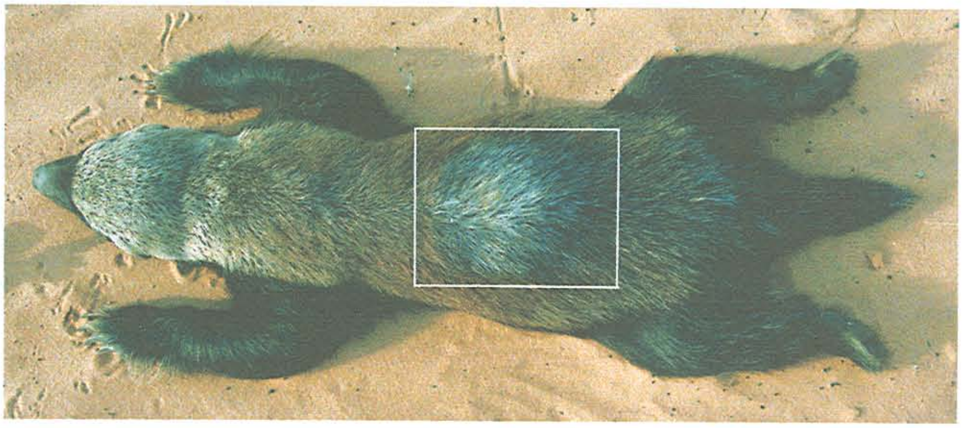

Plate 7.2 Prominent scar in the middle of the back of an adult male honey badger (Am9). The area of thickening measured 13.6 cm x 15 cm with an inner area of white hair.

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).

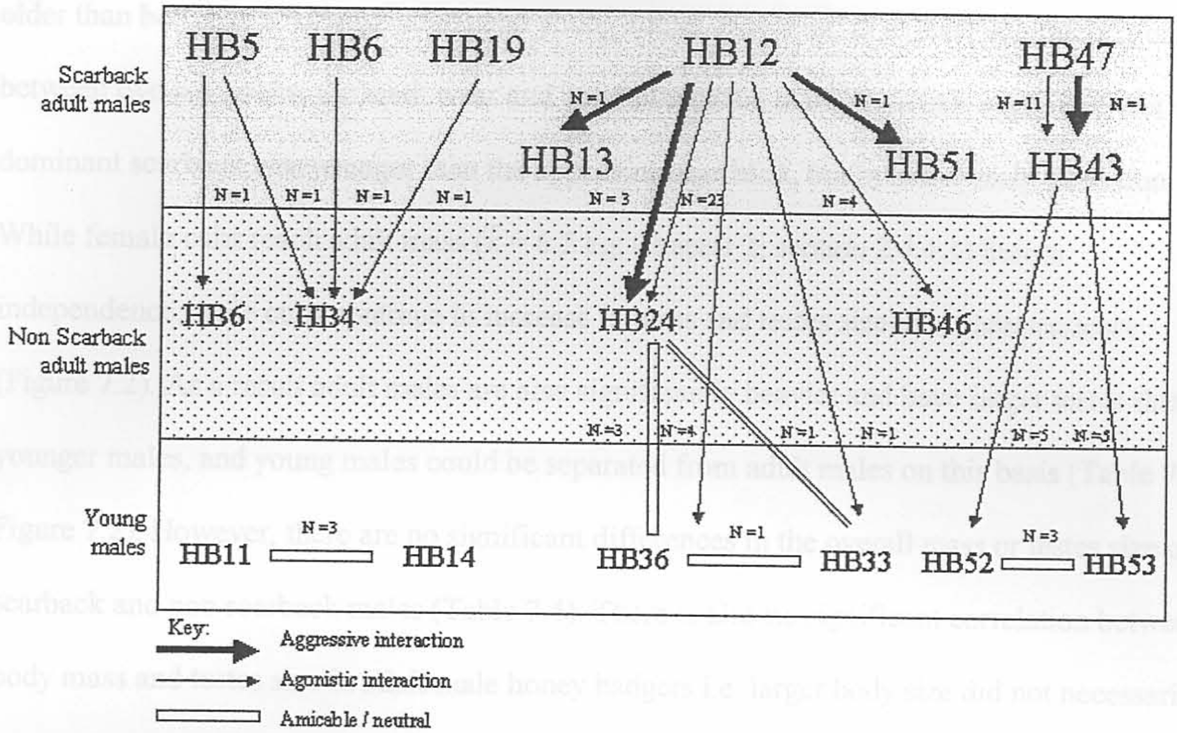

Figure 7.1 Paired aggressive, agonistic and amicable interactions observed between known male honey badgers of different age classes in the KTP. The arrows move from a dominant to a subordinate individual.

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).

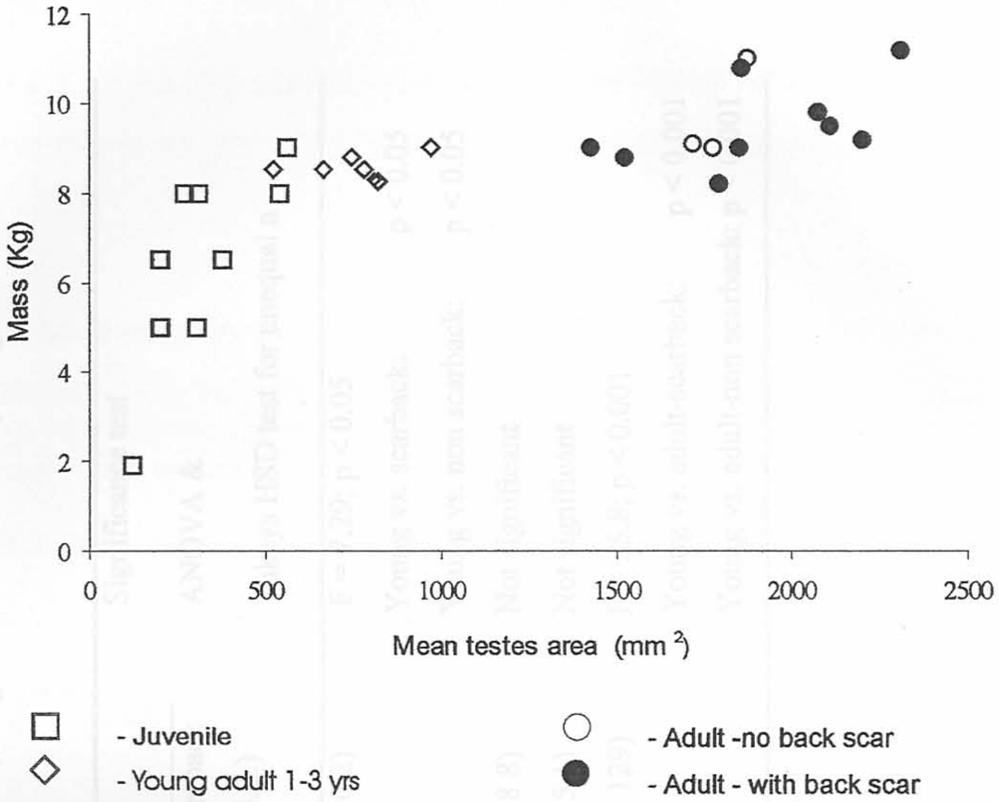

Figure 7.2 Relationship between male honey badger mass, testes area and age category, showing the increase in testes size after independence associated with a change from the young to adult male age category. Scar back males could not be distinguished from non scarbacks on the basis of testes area or 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 = $[(length_{right} \times breadth_{right}) + (length_{left} \times breadth_{left})] / 2$.

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).

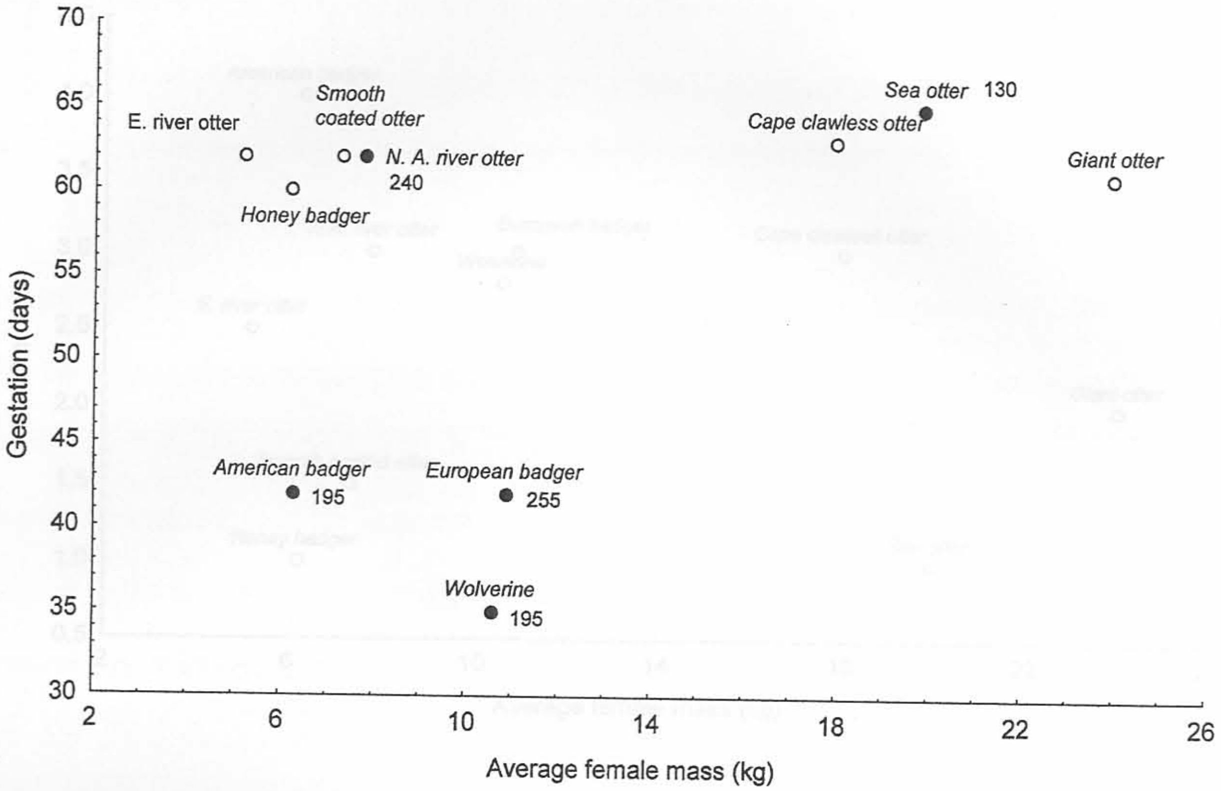

Figure 7.3 A comparison of the average length of gestation in ten medium sized mustelids (> 5 kg) with the closed circles representing those species that show delayed implantation. The length of the delay (in days) is represented by the number next to name. All data, except for the honey badger, are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

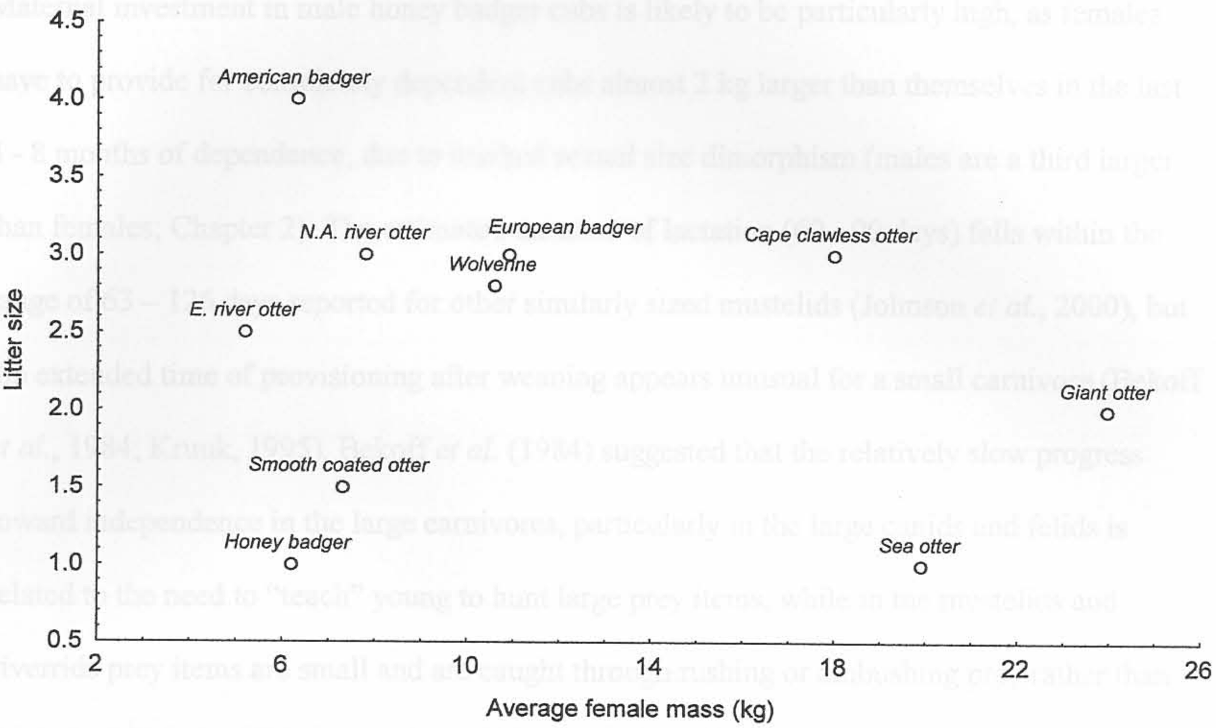

Figure 7.4 A comparison of the litter sizes of ten medium sized mustelid species (adult female mass is > 5 kg) showing the unusually smaller litter sizes of the honey badger, smooth coated otter *Lutrogale perspicillata* and sea otter *Enhydra lutris*. All data except for the honey badger are from Johnson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

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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 Qvarnström & 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 ($\bar{x} = 548\ \text{km}^2$). 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.

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- Chapter 8 -

Summary and conclusions

The Mustelidae is the largest and most diverse family of the Carnivora and while a great deal is known about certain members of the family, others are virtually unstudied (Mcdonald & King, 2000; Bright, 2000). Despite its formidable reputation, extensive distribution and "vulnerable" conservation status, there was a lack of even fundamental biological information on the honey badger *Mellivora capensis.* The objective of this study was therefore to describe the diet, foraging behaviour and social organization of the honey badger and to compare its behaviour with that of other mustelid species. This was achieved through a combination of radio telemetry, spoor tracking and, most importantly, direct observations of habituated individuals. This chapter summarizes the answers to the key questions (section 1.2.4) and in so doing provides an overview of honey badger behaviour in the southern Kalahari.

8.1 What does the honey badger eat and are there sexual and seasonal differences in diet and foraging behaviour?

A recent analysis of interspecific variation and allometry in all the mustelids for which data were available (Johnson *et al.*, 2000), supported the hypothesis that local ecological conditions dictate animal density and spatial organisation, and hence determine social behaviour. The first step was therefore to investigate diet and foraging behaviour as a basis for understanding spatial and social organisation (Macdonald, 1983; Kruuk, 1995).

In the southern Kalahari, the honey badger is a generalist, solitary carnivore with a diverse diet characterized by marked seasonal differences but no sexual differences. In support of optimal diet theory, the honey badger appears to switch between alternative prey species depending on which are currently the most abundant on a daily and seasonal level. In addition there is an increase in dietary diversity in the lean season (cold-dry) in response to a decrease in the availability of preferred prey species. Decreased consumption rates in the cold-dry season are countered by an increase in the time spent foraging with the result that there are no significant seasonal differences in the biomass ingested per kg of body weight in either sex.

In this wilderness area, the honey badger shows a strong seasonal shift from predominantly nocturnal activity in the hot-wet and hot-dry seasons to more diurnal activity in the cold dry season. While the factors affecting the activity patterns of the honey badger are undoubtedly complex and interrelated, this seasonal shift in the timing of activity appears to be primarily due to the honey badger avoiding extreme temperatures by taking refuge in a hole, and not due to a seasonal shift in prey activity.

8.2 How does the honey badger interact with other species, with particular reference to the reported foraging associations?

Interspecific interactions between the honey badger and other mammalian and avian predators were common and included intraguild predation and interspecific feeding associations with seven other species (two mammals and five birds). The most common foraging associations were between the pale chanting-goshawk *Melierax canorus* and the black-backed jackal *Canis mesomelas*. These associations appeared to be facultative commensalism with the associating species benefiting directly through increased intake rate and increased hunting opportunities provided by the rodents and reptiles that escape while the honey badger is digging. The associations did not appear to be either beneficial or detrimental to the honey badger.

Aggressive interactions between sympatric mammalian carnivores could largely be predicted by relative body size. The adults and juveniles of the smaller carnivores (< 1 kg) are all prey of the honey badger, as are the young of medium sized carnivores (1 –12 kg). In turn, the honey badger is killed by lion *Panthera leo*, leopard *Panthera pardus* and possibly spotted hyaena *Crocuta crocuta.* It generally avoids confrontation but when surprised at close quarters it utilizes a formidable and frequently successful threat display to dissuade potential predators, including the release of scent from the anal scent glands, a rattling-roar and rushing movements towards the aggressor.

8.3 Does the honey badger support the typical mustelid pattern of intra-sexual territoriality (Powell, 1979)?

It is generally agreed that in solitary carnivores, the limiting resource for females is food while the limiting resource for males is receptive females. Female home ranges were extensive (138 km^2) and well beyond the upper confidence limits described by the regression of female body mass and home range area for all non social mustelids (Johnson *et al*., 2000). Home range size has been found to be inversely proportional to available prey biomass, and it is likely that the extensive home ranges of female honey badgers are largely a consequence of low prey availability in this semi-arid environment. Since females are accompanied by dependent young for an extended period (12 –16 months), home range area may also reflect the area required to support a "group mass" of a mother and her large cub (12 – 14 kg) rather than just an adult female alone (6 kg).

While neighbouring female home ranges overlap an average of 25 %, females appear to avoid each other temporally through scent marking (token urination), and home range centers are more regular spaced than random. The female spacing pattern therefore resembles a form of intrasexual territoriality although the extensive ranges are not actively defended.

The intersexual difference in home range size is larger than predicted from body size and metabolic considerations alone and adult males appear to be limited by receptive females, as has been found in most carnivores. Adult males have extensive overlapping home ranges (548 km^2) that encompass the home ranges of at least 13 females and do not support the typical mustelid pattern of intra-sexual territoriality.

8.4 How is the spacing pattern maintained?

As has been found in other solitary carnivores, scent marking is an important form of communication in the honey badger, with urine, faeces and secretions from the anal gland regularly used to mark objects in the environment. Both sexes were observed to scent mark frequently but in significantly different ways with adult males predominantly marking at latrines and females and young males using token urination with irregular latrine visits.

Since token urination occur in holes along the foraging path, it is likely that the recipients are intensively foraging honey badgers. It is suggested that token urination allows female and young male honey badgers to partition resource utilization and mediate spatio-temporal separation. The function of latrine visits in females appears to be to advertise their receptive status to males and to gain information on the males in the area (possibly through scent matching; Gosling, 1982). Males use latrines to find females and to advertise their status to other males through scent matching. The "scent matching" hypothesis (Gosling, 1982) suggests that subordinates are able to make an olfactory association between the dominant individual and marking frequency, and this allows the subordinate to identify the dominant individual when they meet and thereby avoid potentially costly aggressive interactions.

8.5 What is the mating system of the honey badger?

As suggested by the spacing patterns, sexual size dimorphism and lack of parental care in males, the honey badger shows a polygynous mating system in common with the majority of the smaller mustelids (Johnson *et al.*, 2000). In contrast to the classical view of polygynous systems, females also appear to play an active role in mate choice, and there is some evidence to suggest that females mate with more than one male in a single receptive period (promiscuous).

Asynchronous breeding and the long interbirth interval result in a skewed operational sex ratio with fewer receptive females than males at any time. For males, receptive females are therefore an unpredictable and scarce resource in space (large home ranges, moving targets) and time (no breeding season), with a long time to renewal. As a result, males adopt a roaming rather than a staying tactic, and instead of territoriality males compete directly for each mating opportunity.

Direct interactions are characterized by ritualized intimidation and appeasement postures, and since individuals retained their intimidation or appeasement roles towards each other on subsequent encounters, there appears to be a non-linear dominance hierarchy loosely based on age, mass and testes size. The dominance hierarchy appears to be maintained through direct interactions and regular scent marking events. In addition to dominance and aggressive display, there is also some evidence that less obvious forms of sexual selection might be important i.e. competitive searching, sperm competition (mate guarding, frequent copulation and sequestering) and infanticide.

8.6 Does the honey badger show sexual size dimorphism and to what extent?

In common with most mustelids the honey badger shows marked sexual size dimorphism, with males a third larger than females with no overlap. Two main theories have been suggested to account for this. The first claims that dimorphism reduces intersexual competition for food by enabling the sexes to exploit different prey, while 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 provided little evidence for the first hypothesis as the sexes did not differ in prey type, prey size or foraging behavior. There is, however, some support for the sexual selection hypothesis as males compete directly through a dominance hierarchy, where heavier males are frequently dominant over lighter males, and indirectly through competitive mate searching, where larger size may confer an advantage of increased mobility (longer legs).

8.7 Conclusions

While the honey badger occupies a unique position as the single extant species in its own genus and subfamily *Mellivorinae*, little information has been available, until now, to compare the behaviour of the honey badger with the other mustelids. At least in the southern Kalahari, the honey badger is non social with marked sexual size dimorphism and a polygynous or promiscuous mating system. In common with the European otter *Lutra lutra*, the honey badger appears to be a relatively "k-selected" species within the Mustelidae, with a small litter size, extended period of cub dependence, increased maternal investment and a relatively short life span. An important factor affecting honey badger spacing and mating patterns is this long period of cub dependence as it results in non seasonal breeding, which in turn affects male spacing and movement patterns and therefore social behaviour.

Numerous studies have reported extensive intraspecific variation in spacing patterns between study sites, years, social status and individuals (Johnson *et al*., 2000) supporting the hypothesis that the mating system for a species may be entirely study dependent. It is likely that the future research on the honey badger in a different area will reveal a different pattern, particularly since the honey badger is found in such a wide variety of habitats. Will the home ranges of honey badgers be smaller in more mesic environments? Does the honey badger have more than one cub in more productive environments or does the long period of cub dependency preclude this? These questions have important consequences for conservation as they relate to the minimum area requirements needed to support a viable population and reproductive output.

It is hoped that this study will provide a basis for comparison for future studies of the honey badger in other habitats and that it provides baseline data that can be used in comparison with other mustelids. I firmly believe that knowledge of a species' behaviour is the key to successful conservation efforts while ignorance of behaviour can lead to conservation failures.

8.8 References

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- Appendix A -

An evaluation of the techniques used for the capture, immobilization, marking and habituation of the honey badger *Mellivora capensis*

9.1 Abstract

Techniques used for capturing, marking and habituating honey badgers in the semi-arid Kalahari and more mesic Zambezi Valley are described and evaluated. Honey badgers can be successfully and safely captured in cage nets and on foot in hand nets. Radio collars provide increased signal strength, which is beneficial given the extensive home ranges of adult honey badgers, but radio implants are preferable as they are not damaged by inter- and intraspecific interactions and are more suited to an animal which catches its prey through digging. While freezebranding was a successful technique for recognizing selected individuals that were recaptured, the freezebrands were often difficult to see through the vegetation. Habituation of selected individuals provided a unique opportunity to investigate scent marking and social behaviour through direct observations.

9.2. Introduction

The honey badger, or ratel, *Mellivora capensis* is a medium-sized mustelid that is found across the greater part of Africa, south of the Sahara, extending through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula (Neal, 1990; F. Cuzin, *in litt.* 2001). Despite its extensive distribution the honey badger has not been well studied, yet it has a formidable reputation as a tenacious and aggressive carnivore (Chapter 1). During the course of a comprehensive study of the feeding ecology and social organisation of the honey badger it was necessary to locate and identify individual animals at frequent intervals. In a preliminary study, Kruuk & Mills (1983) showed that individuals can move as far as 27 km in a day, and they suggested that honey badgers might be considered nomadic. Radio telemetry was therefore considered crucial for locating individuals and for collecting information on home range and movement patterns. Both radio collars and intraperitoneal radio implants have been used successfully on other mustelids (river otters *Lutra lutra:* Melquist & Hornocker, 1979; mink *Mustela vison:* Eagle *et al.*, 1984).

Individual field recognition was also important and since honey badgers do not have external pinnae, ear tagging was not possible. Freeze branding, or cryo-branding, was considered as a suitable alternative as it is considered cost effective and long lasting (Rood & Nellis, 1980) and has been successfully achieved on mongoose species and other small mammals (Rood & Nellis, 1980). Finally, habituation of selected individuals was considered essential to gain an understanding of foraging and social behaviour through direct observations.

This paper provides detailed information on the methods of capture, immobilization, marking and habituation applied while studying the feeding ecology and social organization of the honey badger in the southern Kalahari. Additional previously unpublished information on the capture and marking of honey badgers during a preliminary study in Mana Pools National Park, Zimbabwe is also included (K. Begg, pers. comm.).

9.3. Study area

9.3.1 Kgalagadi Transfrontier Park

The main 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 and neighbouring Gemsbok National Park, Botswana. It is a semi desert region and is described by Acocks (1988) as the western form of Kalahari Thornveld with a very open savanna of *Acacia haemotoxylon*, *Acacia erioloba* and desert grasses. This study was primarily conducted in the central dune area, which is characterized by medium to high dunes on reddish sands where *A. haemotoxylon* appears in a shrub like form with occasional *Boscia albitrunca* and *A. erioloba* trees (Van Rooyen *et al.*, 1984.).

9.3.2 Mana Pools National Park, Zimbabwe

A preliminary study of honey badgers took place from October 1994 to February 1995 in Mana Pools National Park (MNP), Zimbabwe (Begg, 1995), an area of 2196 km^2 in the middle Zambezi Valley in northeastern Zimbabwe. The area is characterized by mature riparian (*Acacia albida* dominated) woodland growing on alluvium, with riverine thickets occurring along the tributaries. Further south, extensive areas of Mopane *Colophospermum mopane* woodland occur as well as tracts of "Jesse bush" (dense *Commiphora sp.* and *Combretum sp*. dominated thickets) growing on acidic, sandstone-derived soils (Dunham, 1992). Visibility is poor particularly during the single highly variable rainy season extending from November to April with an average rainfall of 760 mm.

9.4 Methods

9.4.1 Capture techniques

9.4.1.1 Nets

A permit for the capture of live honey badgers was obtained from South African National Parks Board. In the KTP, tourists and staff do not commonly see the honey badger and there were no known areas (i.e. refuse bins, water points) that were regularly visited by honey badgers. The lack of a central attraction point and the extensive open habitat precluded the use of cage traps. Sandy tracks and firebreaks running through the central study area were routinely driven at 10 -25 km /h at regular intervals during the study period and fresh (< 24 hrs) tracks of a honey badger that had crossed the road transects were identified by a Khomani-san tracker (K. Kruiper). The tracks were followed on foot by the tracker and one researcher until the honey badger(s) were in sight. Honey badgers were then approached downwind to within 10-50 m, chased and caught in hand nets.

Capture nets were made from polyethylene cargo mesh (area 2 m x 2 m; mesh sizes = 50 mm^2 x 3 mm; 100 mm^2 x 8 mm) sewn with 3 mm nylon braid onto a hoop (diameter = 500 mm) constructed from 10 mm steel round bar, and attached to a 1,8 m aluminium handle (diameter = 30 mm).

Captured individuals were wound up inside the net to minimize their movement and immediately hand injected in the rump with an immobilizing drug (section 9.4.2). When a radio collar needed to be replaced or removed (e.g. for an abdominal implant) the honey badger was located by radio tracking and caught in the same manner.

9.4.1.2. Drop door traps

In MNP honey badgers regularly raided refuse bins within the campsite. Two baited drop door cage traps (50 cm x 50 cm x 120 m) made from expanded metal were set in close vicinity to concrete refuse bins. Three smaller baited drop door cage traps (50 cm x 90 cm x 50cm) were made from weld mesh and designed to fit inside these refuse bins. The cage traps were custom made with a single sliding door and baited with a variety of food i.e. lightly fried beef fat, smoked fish, chicken, maize meal and honey). The traps were set from October - November 1994 and August - September 1995) and were repeatedly checked throughout the night. Captured individuals were hand injected through the side of the cage for immobilization. Following study and radio marking the honey badger was allowed to recover in the cage until it was sufficiently awake to be safely released at the capture site.

9.4.1.3 Darting

On one occasion a Co^2 rifle (Dan-inject JM Standard model) was used to inject a habituated honey badger in the KTP by means of a standard (10,5 mm; 1,5ml capacity) dart syringe. Co^2 pressure can be individually adjusted for each shot with a manometer for short range and low impact hits.

9.4.2 Immobilization

All captured honey badgers were immobilized in the field so that they could be easily handled. Two kinds of dissociative anesthetics (Cyclohexylamines) were used during capture. Zoletil ^{R} (Tiletamine hydrochloride with the Benzodiazephine derivative Zolazepam in 1:1 combination) or Ketalar ^{R} (Ketamine hydrochloride). Both have a wide safety margin, and the former is considered to be three to four times more potent than Ketamine (McKenzie, 1993). The sedative neuromuscular blocking agents Rompun ^{R} (Xylazine hydrochloride) and Domitor R (Medetomidine) were always used in conjunction with Ketamine to counter the associated increase in muscle tone commonly associated with use of this type of anesthetic. The alpha-2-agonists RX821002A and Antisedan ^{R} (Atipamezole) were used to reverse the effects of the Rompun and Domitor respectively.

9.4.3. Marking

9.4.3.1 Radio collars

In the MNP captured honey badgers were fitted with AVM transmitters (AVM Instrument Company, California), custom built by the Mammal Research Institute (M. Haupt; Department of Zoology and Entomology, University of Pretoria). In the KTP, individuals were fitted with Telonics MOD 400 (180 grams) or MOD 335 (105 grams) radio collars (Telonics telemetry-electronics consultants, Arizona). All transmitters were attached to a Telonics CLM collar (width = 4 cm; adjustable range = 27 cm – 35 cm) with a CAT-1 protective casting and a 20 cm external flexible whip antenna (Telonics; TA-5 HFT). In four collars the full length of the external antenna was entirely sewn within a butyl tab to increase strength and prevent the antenna from breaking off at the point of exit from the collar. To increase battery life (from 19 months to 22 months) the pulse rate was reduced from 70 pulses / min to 60 pulses / min. A beta-light was fastened onto the upper surface of one collar to test the feasibility of using beta-lights to follow honey badgers at night, as had been achieved in studies of the brown hyaena *Hyaena brunnea* (Mills, 1990) and European badgers *Meles meles* (Kruuk, 1989).

9.4.3.2 Intraperitoneal implants.

In both the MNP and KTP studies, selected individuals were surgically implanted with intraperitoneal radio implants IMP/400/L (Telonics; 31 mm x 94 mm) and IMP-2 (Merlin Systems; 19 mm x 105 mm) in the field, by wildlife veterinarians. The Telonics IMP/400/L has been used effectively in coyote, otter, beaver, African wild dog, and aardwolf (M. Ben-David pers. comm.; P. Richardson pers. comm.). Each implant was inserted through a 45mm incision into the peritoneal cavity and was "free floating", allowing the implant to stabilize on its own. All implants were soaked in a disinfectant (15 % Hibitane solution) for 24 h prior to surgery and rinsed in sterile water directly before implantation. Two layers of single interrupted sutures closed the wound. Animals were injected with penicillin (approximately 2 cc) before release, placed in a hole to recover and were monitored from afar with binoculars.

9.4.3.3 Freeze branding

Honey badgers captured but not radio-marked were individually marked with a freeze brand for possible later identification in the field. In addition, three radio-marked individuals were freeze branded to assess the success of the technique. Following immobilization, an area of black fur (approx. 40 mm x 40 mm) was clipped on either the shoulder or rump, shaved and cleaned with ethanol. A small (20 mm diameter) cardboard hexagon was pressed against the skin as a template. "Histofreezer" (Koninklijke Utermohlen, The Netherlands) is a cryosurgical aid used primarily by dermatologists for removal of verrucae and consists of a liquefied cryogenic gas composed of dimethyl ether and propane in a small gas canister (125 ml) with applicators. The "Histofreezer" nozzle was held gently against the skin, with the freezing agent sprayed liberally onto the skin for varying amounts of time (15 sec – 30 sec) within the template.

9.4.4 Age determination and classification

No information on ageing in honey badgers is available. For this reason the age classes used in the KTP study are presented in detail. While counting cementum annuli in teeth is known to be an accurate method of age determination in other carnivores (Kruuk, 1995), the absence of material from known age individuals for comparison and the problems with using cementum annuli in an animal living in a non-seasonal environment (Harris *et al.*, 1992) precluded using this method in this study. Since tooth wear alone is known to show large differences both between individuals and in different habitats (Harris *et al.*, 1992), information on behaviour, size and condition were also assessed. To minimize error, honey badgers were simply divided into four broad categories, den cub (0-3 months), foraging cub (3 months to independence), young adult (age 1-3 yrs), and adult (older than three years; Table 9.1).

Cubs younger than 3 months were never captured as they remained in the den and these cubs were categorized primarily by their behaviour and estimated length in relation to the adult female e.g. length of the female's head. In adults tooth wear was most noticeable on the third incisor on the upper jaw, which in young adults is noticeable different to other incisors and resembles a canine (Plate 9.1b & c), but is quickly worn down to resemble the other incisors in older badgers. It is likely that teeth of Kalahari honey badgers wear down more rapidly than teeth in other areas due to the abrasive action of the sand, as has been suggested for the brown hyaena *Hyaena brunnea* (Mills, 1990) in the same habitat.

Table 9.1: Descriptions of the age categories used in this study to assess captured honey badgers.

Age category	Overall description	Tooth wear
Den cub 0-3 months	Not foraging with mother, remained in den, < 30cm long. Obtain black& white colouration at 1 month.	"Milk" or deciduous teeth erupting
Foraging cub 3-16 months	Weaned but still dependent on mother for food, initially smaller than mother but reached adult dimensions at about 8 months (Figure 8.2). May be larger than adult female if cub is male. Bright white mantle.	Ranged from teeth still erupting (Plate 9.1a) to permanent teeth (Plate 9.1b) with no wear.
Yearling Est. 1- 3 yrs	Independent, few scars on body and in males no back scar and small testes (Plate 6.2a)	Slightly worn teeth, most noticeable on 3rd incisor and canines (Plate 9.1c)
Adult Est. 3- 8yrs	Presence of scars, In males large testes, and in older males a prominent back scar. White mantle appears to darken with age.	Moderate (Plate 9.1d) to extensive (Plate 9.1e & f) tooth wear, on all teeth. 3rd incisor no longer pointed. In older individuals teeth were frequently missing or rotten.

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[1] Adult study animals followed for more than 2 years were seen to age considerably in this time i.e. teeth wear, loss of condition.

A) Foraging cub
Milk teeth -, approx. 6mths old

B) Foraging cub
Permanent teeth - 16mths old

C) Young adult

D) Adult

E) Old adult

F) Old adult

Plate 9.1: The teeth (primarily canines and incisors) of the honey badger from three age classes based on tooth eruption and wear from the KTP. Note the wear on the third incisor on the upper jaw. The worn incisors and canines of two individuals (Plate 9.1E & 9.1F) that were considered old are also shown.

9.4.5 Habituation

The openness of the KTP vegetation lends itself to visual observation (Mills, 1990). Habituation was attempted on seven radio-marked females and five radio-marked males with a goal to follow individuals in a vehicle without any obvious influence on their behaviour. On no occasion were individuals fed as it was considered likely that this would create a positive (not a neutral) association with the vehicle. The vehicle was parked on a dune crest within sight and smell of a selected honey badger in a hole (± 100 m) and remained in this position until the honey badger (s) left the hole. Each time the honey badger left the hole the engine was started, but no approach was made. After a number of attempts, the individual left the hole and moved on without running back into the hole. Initially the distance of 100 m or further was maintained whilst following the honey badger (often ahead out of sight) and the engine was kept running at all times. The objective being to allow the individual to become accustomed to the engine noise and not to threaten the animal by advancing towards it. Initially the honey badger was encouraged to dig and eat without the vehicle approaching, and then gradually the distance was reduced until individuals could be followed from 10-15 m away without any obvious effects on the behaviour of the honey badger. In the final step, inidvduals were habituated to the engine being turned on and off whilst they were foraging. On no occasion were they followed on foot and while researchers did sit on the vehicle roof or on the bonnet, they always remained within the vehicle silhouette

9.5 Results & Discussion

9.5.1 Capture success

9.5.1.1 Nets

Hand nets were used to catch honey badgers 69 occasions. This technique was considered highly efficient, with a minimal amount of stress and little potential for harm compared to the other methods e.g. dart, cage trap. On 22 captures individuals were located through spoor tracking, while radio tracking was used to relocate individuals for capture on 43 occasions, including three captures at night. Twenty non radio-marked individuals (cubs and accompanying adults) were caught when they were observed with radiomarked individuals and four honey badgers were caught after an opportunistic sighting.

The honey badger can not outrun a reasonably healthy person over a short distance (< 80 m) and will frequently turn to face the aggressor, affording an ideal opportunity for capture. On one occasion a female and large male offspring were caught in the same net. The larger net design was considered inappropriate (mesh size = 100 mm^2 x 8 mm) as a female and her offspring could escape through this mesh size and it was considered unnecessarily heavy. Although honey badgers can bite through the finer 3 mm polyethylene net, they were never observed to escape from the net as immobilization was almost immediate. For habituation purposes, no vehicles were allowed near (< 500 m) the scene of capture until the honey badger was completely immobilized. On one occasion a female honey badger was caught with the vehicle close by and this female could not be habituated.

9.5.1.2 Cages

In the MNP honey badgers were regularly seen scavenging in four concrete refuse bins in the Nyamepi tourist camp and within the staff accommodation quarters (particularly when fish was being smoked). Trap success was 29.6 % (n = 8; 27 trap nights). During the nine nights when traps were set, honey badgers were sighted on 16 occasions in the immediate vicinity (>500 m) of the traps. The main draw back of this technique was that it was non selective as three individuals were recaptured and one African civet *Civetticitis civetta* and one small spotted genet *Genetta genetta* were trapped. Captured honey badgers appeared considerably calmer inside a drop door cage compared to other canids, felids and viverrids (pers. obs.).

9.5.1.3 Darts

On one occasion a habituated honey badger (Am 4) was darted from a vehicle at close range (± 6 m). The first dart missed due to the typically unpredictable movements of the honey badger. The second dart was placed in the upper thigh area; the honey badger ran off after a defensive rattle and was relocated 12 minutes later immobilized above ground. This technique is generally not considered advisable due to the risk of the honey badger going underground before being immobilized. There was also a significant risk of missing the small target area (shoulder or thigh) and potentially harming the honey badger. The honey badger did not appear to associate the vehicle with the dart and remained habituated after capture.

9.5.2 Immobilization

Honey badgers were chemically immobilized on 73 occasions (MPP= 5; KTP = 68). Only one fatality was recorded after immobilization as a result of heat stress (ambient temperature 36°C) during the recovery period. To immobilize the honey badger using Ketamine, McKenzie (1993) suggested 5-6 mg / kg, plus Xylazine at 0,5 mg / kg but in MNP higher doses (8.5 – 18 mg / kg; average 17 mg / kg) were required for successful immobilization of five adult male honey badgers. This is comparable to the dosages required (17 – 25 mg/kg) to immobilize the wolverine *Gulo gulo* (Hash & Hornocker, 1980). Recumbency occurred within three to four minutes and honey badgers were immobile for 60 - 95 min. In conjunction with Ketamine, a dose of between 1 – 12 mg / kg of Xylazine or 0,1 mg / kg of Medetomidine was also administered.

When using Zoletil, the suggested dosage was 2 - 3 mg / kg for the honey badger (Schobert, 1987; McKenzie, 1993). In the KTP, Zoletil was used successfully used on 67 occasions in the KTP with dosages ranging from 2.7 mg / kg to 9 mg / kg ($\overline{x} = 5.2$ mg / kg). It should be noted that some of the higher doses were due to Zoletil being used months after reconstitution. Honey badgers typically recovered after 50 -180 min ($\overline{x} = 71$ min; n = 18). The eyes were covered with a dark cloth to prevent eye damage from sunlight and to prevent stimulation from movement. During recovery, a hole (± 50 cm deep) was dug in the shade of a bush and the sedated individuals were placed in this hole with a few branches covering the entrance to provide shade.

9.5.3. *Marking*

9.5.3.1 Radio-marking

Radiomarking was considered essential as the honey badger does not return to a fixed den site and can move up to 40 km in 4.3 h (Chapter 5). Honey badgers were radio collared on 32 occasions (MNP = 2; KTP = 30). The transmitters from both radio collars fitted in the MNP were broken by the honey badgers within 10 days and individuals could no longer be located. Eight of the Telonics radio collars received serious aerial damage within four to seven months, with the external aerial cable broken off at the point of exit from the collar. For this reason collars were removed or replaced with implants within six months, although in one case a collar remained in tact for 15 months. To prevent aerial damage a butyl tab was sewn (± 25 cm) along the external portion of the aerial. This delayed breakage but after a few months the stitching wore out on these tabs. All collars were removed from honey badgers before the end of the battery life or at the end of the study period.

A total of 17 honey badgers were implanted (MPNP =3; KTP = 14). Both Merlin implants failed immediately despite intensive above ground tests and these individuals were never relocated. In contrast, only one of the 15 individuals implanted with Telonics implants was never relocated after implantation. Eight females (5.8 kg – 7,1 kg) were implanted and three were known to conceive and give birth after implantation. Implants lasted the full duration (20 – 22 months) and it was decided that they should not be removed since this would increased the chances of post-surgical infection and implants were frequently encapsulated within the abdomen wall (D. Grobler pers. comm.). On one occasion an implant was recovered from individual that was killed by a leopard and it showed no sign of wear. Since the honey badger appears to be short lived (3 - 8 years) in the wild, implants are considered to be of minimal threat to the individual.

Overall implants are considered preferable to collars in the honey badgers due to their active digging lifestyle and regular intra- and inter-specific interactions. However, radio implants provided a significantly weaker signal and individuals were more difficult to locate from the ground. This is an important consideration given that females have a mean home range size of 138 km^2 and males, 548 km^2 (Chapter 5). Radio collars are particularly useful for the initial few months after capture as they immediately provided information on the area use of an individual but should be replaced with implants within 3-4 months.

9.5.3.2 Freeze branding

In freeze branding the pigment producing melanocytes in the hair follicles are killed, and hair that regrows at the frozen site is white (Rood & Nellis, 1980). Freezebranding provides an effective, permanent, and in the black and white honey badger, a relatively unobtrusive method of marking individuals. In the KTP a total of 15 honey badgers were freeze branded on the shoulder or thigh. Eight individuals were never adequately re-sighted or recaptured to determine the success of this technique. One honey badger was freeze branded for 15 sec, which resulted in no visible change while a freeze brand of 20 sec resulted in a pale discoloration of the skin, but no white regrowth of the hair. Three individuals branded for 25 sec showed variable amounts of white hair regrowth. The freeze brands of two individuals branded for 30 sec were very successful, resulting in a clearly noticeable white patch of fur within two months of marking. This technique proved useful for recognizing individuals less than 50 m meters away, but freezebrands were difficult to see in dense vegetation.

9.5.4. Habituation

Direct observations allowed events such as scent marking and prey capture to be described in the behavoural contexts in which they occurred. More than 2000 h of effort were required to successfully habituate nine radiomarked honey badgers (five females with five cubs, four males). On average habituation took 14 days with large individual differences. In general males appeared easy to habituate than females and females with young cubs were the most difficult. The key to successful habituation was to separate the factors associated with capture from habituation (i.e. capture on foot vs. habituation to a vehicle) and to maintain a continuous presence for at least the first ten days. Two females could not be habituated within a reasonable time frame. The one individual was initially captured with the vehicle and would bolt into a hole at the vehicle's approach and the other had a small cub (< 3 months old). In all individuals it was necessary to visit habituated individuals at least every 6 weeks to maintain a workable level of habituation. Habituated individuals were visually observed for 5811 h, and continuous observations of selected individuals provided detailed information on sexual and seasonal differences in diet, foraging behaviour, movement patterns, scent marking and inter- and intra-specific interactions.

9.6 References

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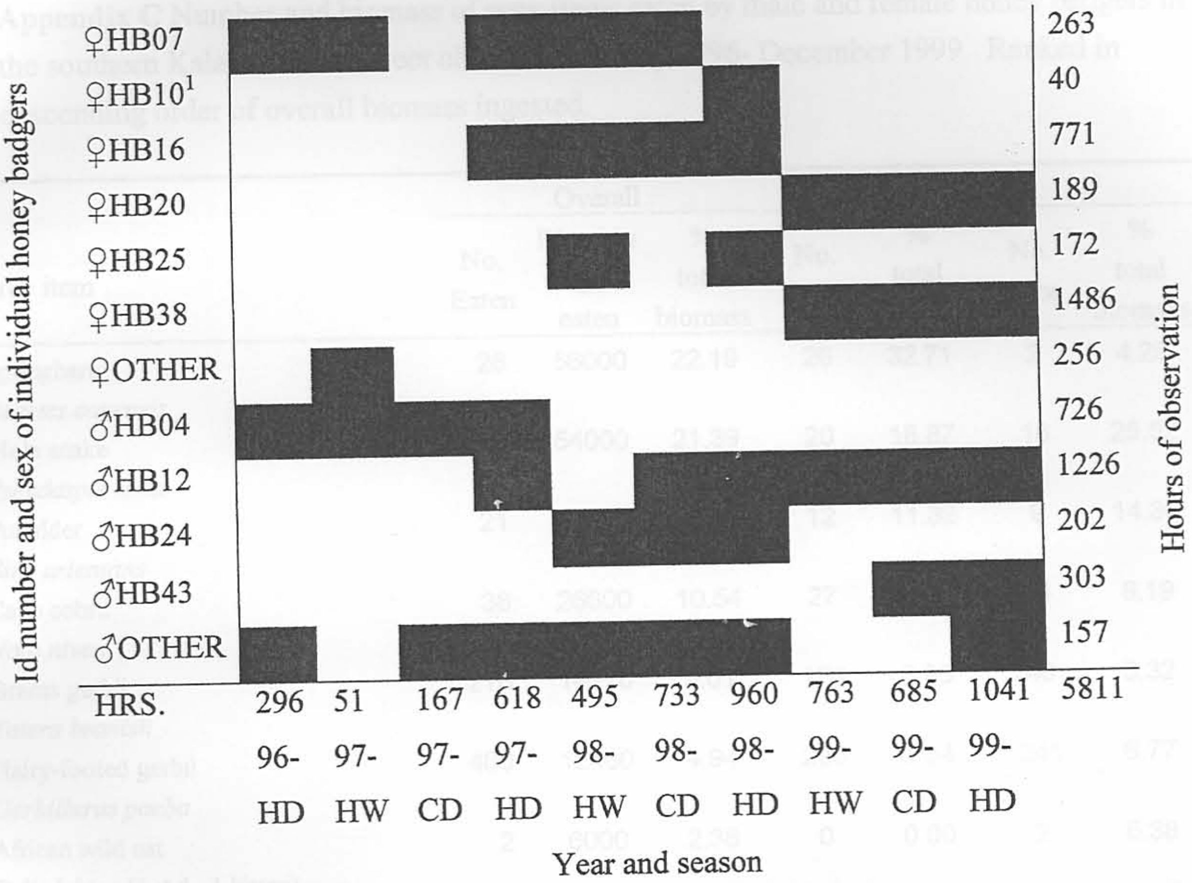
- Appendix B -



Appendix B: Year, season, and number of hours individual habituated honey badgers were directly observed in the KTP from 1996 - 1999. Where HB10 was the habituated cub of HB16 that was followed for a brief period after independence before she moved out of the study area

- Appendix C -

Appendix C Number and biomass of prey items eaten by male and female honey badgers in the southern Kalahari from direct observations: July 1996- December 1999. Ranked in descending order of overall biomass ingested.

	Overall			♀		♂	
Prey item	No. Eaten	Biomass (g) eaten	% total biomass	No. eaten	% total biomass	No. eaten	% total biomass
Springhare *Pedetes capensis*	28	56000	22.19	26	32.71	2	4.25
Mole snake *Pseudaspis cana*	36	54000	21.39	20	18.87	16	25.52
Pufadder *Bitis arientans*	21	31500	12.48	12	11.32	9	14.36
Cape cobra *Naja nivea*	38	26600	10.54	27	11.89	11	8.19
Brants gerbil *Tatera brantsii*	218	14170	5.61	170	6.95	48	3.32
Hairy-footed gerbil *Gerbillurus paeba*	480	12480	4.94	235	3.84	245	6.77
African wild cat *Felis lybica* (1 Ad., 1 kitten)	2	6000	2.38	0	0.00	2	6.38
Horned adder *Bitis caudalis*	22	4400	1.74	11	1.38	11	2.34
Common barking gecko *Ptenopus garrulous*	845	4225	1.67	631	1.98	214	1.14
Cape fox *Vulpes chama (cubs)*	5	4000	1.58	1	0.50	4	3.40
Scrub hare *Lepus saxatilis*	2	4000	1.58	0	0.00	2	4.25
Yellow mongoose *Cynictis penicillata*	6	3480	1.38	4	1.82	2	1.23
Solitary bee larvae *Parafidelia friesei*[1]	84	2983[3]	1.18	3	0.1	81	3.17
Striped mouse *Rhabdomys pumilio*	88	2816	1.12	26	0.52	62	2.11
Sand snakes *Psammophis sp.*	14	2800	1.11	11	1.38	3	0.64
Giant ground gecko *Chondrodactylus angulifer*	111	2553	1.01	78	1.13	33	0.81
Pale chanting goshawk *Melierax canorus* (chicks)	5	2500	0.99	0	0.00	5	2.66

Appendix C cont.

Prey item	Overall			♀		♂	
	No. Eaten	Biomass (g) eaten	% total biomass	No. eaten	% total biomass	No. eaten	% total biomass
Kalahari tree skink *Mabuya occidentalis*	198	1980	0.83	8	0.88	190	0.74
Striped polecat *Ictonyx striatus*	3	2100	0.78	2	0.05	1	2.02
Black korhaan *Eupodotis afra*	3	1800	0.71	2	0.75	1	0.64
Bat-eared fox *Otocyon megalotis (1SA,1cub)*	2	1600	0.63	1	0.50	1	0.85
Suricate *Suricata suricatta*	2	1400	0.55	1	0.44	1	0.74
Honey badger (cub) *Mellivora capensis*	2	1000	0.40	0	0.00	2	1.06
Yellow scorpion *Opistophthalmus wahlbergii*	190	950	0.38	177	0.56	13	0.07
Bibrons stilleto *Atractaspis bibronii*	6	900	0.36	4	0.38	2	0.32
Adder sp.	4	800	0.32	1	0.13	3	0.64
Brants‘ whistling rat *Parotomys brantsii*	9	720	0.29	8	0.40	1	0.09
Bicoloured quill-snouted snake *Xenocalamus bicolor bicolor*	3	600	0.24	3	0.38	0	0.00
Namaqua sandgrouse *Pterocles namaqua*	2	600	0.24	1	0.19	1	0.32
Spotted eagle owl *Bubo africanus* (chick)	2	600	0.24	1	0.19	1	0.32
Ant eating chat *Myrmecocichla formicivora*	12	480	0.19	9	0.23	3	0.13
Cape gecko *Pachydactylus bibronii*	27	351	0.14	19	0.16	8	0.11
Barn owl *Tyto alba*	1	300	0.12	0	0.00	1	0.32
Bushveld elephant shrew *Elephantulus intufi*	5	210	0.08	4	0.11	1	0.04
Short-tailed gerbil *Desmodillus auricularis*	4	184	0.07	0	0.00	4	0.20
Spotted eagle owl eggs	3	135	0.06	0	0.00	3	0.16
African rock python (juv) *Python sebae natalensis*	1	150	0.06	0	0.00	1	0.16
Damara molerat *Cryptomys hottentotus damarensis*	3	90	0.04	1	0.04	2	0.06

Appendix C. cont.

Prey item	Overall			♀		♂	
	No. Eaten	Biomass (g) eaten	% total biomass	No. eaten	% total biomass	No. eaten	% total biomass
Common quail *Coturnix coturnix*	1	95	0.04	1	0.06	0	0.00
Termites (alates) *Hodotermes mossambicus* (34 individuals)[1]	1	68	0.03	1	0.02	0	0.00
Beetle: Scarabaeidae; subfamily:Melolonthinae (31 individuals) [1]	4	62	0.02	1	0.00	3	0.06
Pygmy mouse *Mus minutoides*	12	60	0.02	5	0.02	7	0.04
Yellow scorpion *Parabuthus raudus*	9	45	0.02	4	0.01	5	0.03
Striped sandveld lizard *Nucras t. tessellata*	4	60	0.02	3	0.03	1	0.02
Ground agama *Agama aculeate*	2	50	0.02	2	0.03	0	0.00
Lark sp.	1	60	0.02	0	0.00	1	0.06
Pouched mouse *Saccostomus campestris*	1	47	0.02	0	0.00	1	0.05
Woosnams desert rat *Zelotomys woosnami*	1	62	0.02	1	0.04	0	0.00
Maggots Order: Diptera-(8 individuals)[1]	1	16	0.01	1	0.01	0	0.00
Black scorpion *Opistophthalmus carinatus*	5	25	0.01	4	0.00	1	0.00
Black/brown scorpion *Parabuthus granulatus or kalaharicus* [2]	3	15	0.01	0	0.00	3	0.02
Black & yellow sand lizard *Heliobolus lugubris*	2	20	0.01	2	0.01	0	0.00
Scaly feathered finch *Sporopines squamifrons*	1	30	0.01	1	0.02	0	0.00
Beetle *Order: Coleoptera*	2	4	0.00	2	0.00	0	0.00
Locust *Order: Orthoptera*	2	4	0.00	0	0.00	2	0.00
Sociable weaver chicks *Philetairus socius* [1]	3	-	-	0	-	3	-
Owl pellet [4]	2	-		0		2	
Snake skin [4]	2	-		0		2	
TOTAL	**2550**	**249405**		**1526**		**1024**	

[1] = Number eaten represents feeding events not individuals.

[2] = Identification of scorpion remains in scats (L. Prendini; Appendix C) showed that honey badgers were eating two species of black scorpion with small pincers, the more common *Parabuthus granulatus* and the endemic *P. kalaharicus*.

[3] = Biomass estimated from time spent feeding at 0.88 larvae/minute

[4] = Prey items assumed to have little biomass value

- Appendix D -

Appendix D Number of hours of observation of habituated male and female honey badgers for each hour of the day in each season in the KTP.

	Hours-♀				Hours-♂			
Time of day	HW	CD	HD	Total	HW	CD	HD	Total
00h00-01h00	46.8	25	67.7	139.5	7	39.7	59.8	106.5
01h00-02h00	45.8	25	64.5	135.3	7	36.3	56.9	100.2
02h00-03h00	44.2	25	64	133.2	7	36.7	54.1	97.8
03h00-04h00	42	25	63.1	131	7	37	50	94
04h00-05h00	41	25	62.5	129	7	37	50	94
05h00-06h00	40.3	25	64	129.3	7	37.7	52.3	97
06h00-07h00	42.3	26	64.5	132.8	7	37.6	59.3	103.9
07h00-08h00	44	27.1	61.8	132.9	7	37.2	59.1	103.3
08h00-09h00	41.6	25.5	57.3	124.4	10.1	40.3	53.4	103.8
09h00-10h00	43.3	25.9	57.4	126.6	10.5	41.4	53.8	105.7
10h00-11h00	44.8	24	58.1	126.9	11.7	45.9	54.8	112.4
11h00-12h00	44.2	20.2	59.4	123.8	11.4	41.2	56.1	108.7
12h00-13h00	40.8	20.5	60	121.3	11	43.7	57.7	112.4
13h00-14h00	39	20.2	60	119.2	11	44.3	58	113.3
14h00-15h00	39	20.3	60	119.3	11.5	44.6	58	114.1
15h00-16h00	39.8	23.5	59.6	122.9	12	45.6	58	115.6
16h00-17h00	40.9	23.3	58.3	122.5	11.2	45.9	59	116.1
17h00-18h00	42.7	23.1	63.6	129.4	10.6	46.3	61.7	118.6
18h00-19h00	43.4	23.0	64.4	130.8	10.3	47.9	61.2	119.4
19h00-20h00	70.2	21.5	64.6	156.3	10.2	44.8	65.6	120.6
20h00-21h00	51.3	24.1	66.4	141.8	10.9	42	65.7	118.6
21h00-22h00	53.7	24.4	71.2	149.3	8.9	42.4	64.2	115.5
22h00-23h00	53.1	24	72.7	149.9	7.6	41.8	65.9	115.3
23h00-00h00	53	36.6	72	161.6	7.7	43.3	65	116
Total	1087	583	1517	3188	223	1001	1400	2623