

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

C. M. Begg^{1,2*}, K. S. Begg², J. T. Du Toit¹ and M. G. L. Mills^{1,2,3}

¹ Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, Republic of South Africa

² Carnivore Conservation Group, Endangered Wildlife Trust, Johannesburg, Republic of South Africa and Private Bag X11, Parkview 2122, South Africa

³ South African National Parks, Kruger National Park, Private Bag X402, Skukuza 1350, South Africa

(Accepted 19 December 2002)

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 kg 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 seasons. In accordance with these predictions, results suggest that the honey badger maintains its intake level by food switching and by 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.

Key words: honey badger, ratel, mustelid, Kalahari, diet, foraging behaviour

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, pers. comm.). Despite its extensive distribution the species has not been well studied. This paper 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 organization (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, pers. comm.) throughout its range, as well as analysis of stomach contents (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, Pulliam & Charnov, 1977; Taylor, 1984). This has been found in other mustelids, i.e. the Eurasian otter *Lutra lutra* (Carss, Elston & Morley, 1998), American marten *Martes americana* (Ben-David, Flynn & Schell, 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

*All correspondence to: C. M. Begg, Postnet Suite 230, Private Bag X18, Rondebosch, 7701, Republic of South Africa. E-mail: ratel@iafrica.com

nutritional requirements (Gittleman & Thompson, 1988; Gedir & Hudson, 2000).

Diet and foraging behaviour may also differ between individuals of different 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 (Moors, 1980; Erlinge, 1981; 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 (Powell, 1979; Moors, 1980; Erlinge, 1981; Sandell, 1989), while larger males are favoured in competition for mates as a result of intrasexual selection (Powell, 1979; Moors, 1980; Gittleman & Van Valkenburgh, 1997; Weckerley, 1998; Begg, 2001).

In the honey badger, the degree of sexual size dimorphism was previously unknown, but in a 6-week study by Kruuk & Mills (1983), differences were observed 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 intrasexual 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 paper 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.

METHODS

Study area

The study started in July 1996 and continued until December 1999 (42 months) in the Kgalagadi

Transfrontier Park (KTP), which encompasses an area of 36 200 km² 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* exists in a shrub-like form with occasional *Boscia albitrunca* and *A. erioloba* trees. Dune areas are interspersed with slightly undulating open plains areas, which have a similar plant composition but with few *B. albitrunca* trees, and pans and yellowish sands, which support shrub veld of *Rhigozum tricophorum* and *Monechma* sp. (Van Rooyen *et al.*, 1984).

Climate

The study area falls between the 200 and 250 mm isohyets and has 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 January to April, when the mean monthly temperature is *c.* 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; the hot-dry season (HD) from September to December when the monthly temperature is *c.* 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 3 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 3 camps (Table 1). All years of the study had comparatively low rainfall, especially 1999 (Table 1).

Data collection

A permit for the capture of live honey badgers was obtained from South African National Parks and all immobilization and sedation was done by K. Begg, who holds a licence for the Chemical and Physical Restraint of Wild Animals (Veterinary course, Harare 1995). Fresh honey badger tracks encountered were followed on foot by a Khomani–San tracker (K. Kruiper) and 1 researcher until the honey badger(s) was in sight. Honey badgers were then approached downwind to within 10–50 m, chased and caught in robust hand nets. Captured individuals (*n* = 67) were wound up inside the net to minimize their movement and immediately hand injected

Table 1. Monthly rainfall records measured at three weather stations in the KTP summarized into seasonal totals (mm) for the period of study: June 1996–December 1999. Seasons: HD, hot-dry; HW, hot-wet; CD, cold-dry

Weather station	Season and year													
	1996		1997				1998				1999			
	HD	Total	HW	CD	HD	Total	HW	CD	HD	Total	HW	CD	HD	Total
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
Twee 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

in the rump with an immobilizing sedative drug, Zoletil® (Tiletamine hydrochloride with the Benzodiazepine derivative Zolazepam in 1 : 1 combination; mean dosage = 5.2 mg/kg). No honey badgers were injured as a result of capture and 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. Honey badgers typically recovered after 50–180 min (mean = 71 min; $n = 18$).

Whilst sedated, 25 individuals (13 females and 12 males) were fitted with Telonics MOD 400 (180 g for adult males weighing 10–12 kg) or MOD 335 radio-collars (105 g for adult females and young males weighing 5.7–7 kg). All collars were removed from honey badgers before the end of the battery life or at the end of the study period. A wildlife veterinarian implanted 10 of the radio-marked adults (5 females and 5 males) and 3 large cubs (1 male, 2 females) with intraperitoneal radio implants (Telonics IMP/400L; 31 × 94 mm). Three of the adult females 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 increase the chances of post-surgical infection and implants were frequently encapsulated within the abdomen wall (D. Grobler, pers. comm.). Since honey badgers seem to be short lived (3–8 years) in the Kalahari, implants are considered to be of minimal threat to the individual. An implant recovered from a female honey badger killed by a leopard 13 months after implantation showed no sign of wear. There was no evidence that any animal died or was injured as a direct result of either radio-collars or radio implants. Detailed methods of capture and immobilization are presented in Begg (2001).

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 claw with the forelimb pulled straight); tail (base of tail to tip) and neck circumference. Over 2000 h were spent habituating 9 radio-marked adult badgers (5 females with 5 cubs and 4 males) to the vehicle until they could be followed without any obvious influence on their foraging behaviour. On occasion, habituation also allowed collection of visual information of non-habituated badgers (termed ‘other females and ‘other males’) as

the non-habituated individuals seemed to take their cue from the habituated badgers and sometimes relaxed in the presence of the vehicle. During the study, 5461 h were spent with habituated badgers (females 2881 h; males 2580 h) with an additional 335 h spent observing ‘other’ honey badgers. Selected animals were followed continuously for observation periods ranging from 1 to 12 days (mean = 4, $n = 91$) with an additional 57 short observation periods (<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 min 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. Since >85% of prey items were caught underground through digging, the spotlight was considered to have minimal effect on the capture success of digging events. When prey items were chased above ground, care was taken not to blind or disorientate the prey items in the spotlight. Where possible the spotlight was moved off both the prey and the badger or both the prey and the honey badger were kept in the spotlight. Honey badgers were observed to move in and out of the spotlight with no change in their behaviour, as they seemed to be hunting primarily using scent.

Rodent trapping was used to assess seasonal changes in the relative abundance (Ra) of small mammals. Eight trap-lines were set each season for 3 years (1997–99) with 3 trap-lines set in dune habitat, 3 in open plains and 2 in *R. tricophorum* patches. Each trap-line consisted of 50 Sherman traps set in a cross formation (25 × 25 traps) where each trap was 15 m from the next. A trap-line was set for 2 nights and 1 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.

Analysis

Prey profitability

For the 10 most common prey species caught through digging, an overall index of relative prey profitability was estimated as average biomass yield per unit digging time. For this analysis, the sampling unit was a single digging event and data from individual honey badgers were pooled. 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. Sometimes the pincers and tail of scorpions were discarded, as were the wing feathers and talons of chicks of large raptors. 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 probably 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.

Seasonal and sexual differences in diet composition

Prey items from visual observations were summarized into 8 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 analysed separately from other prey items since it seems that they were primarily eaten for their water content. 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. 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 min. On 2 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, $N_B = 1/\sum p_i^2$ 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, $H = (\log n! - \sum \log f_i!)/n$ 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 3 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 (generalized 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 individuals for each of the 3 seasons, i.e. hot-wet, cold-dry, and hot-dry.

Where possible parametric tests (analysis of variance, 2-sample, 2-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). Spearman's 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.

RESULTS

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 (Appendix), 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. Hughes & 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. Hughes & 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 defence 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).

Tsama melons

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 >90%. A sample of 20 uneaten tsamas was weighed and the diameter measured to provide 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, c. 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-square test: $\chi^2 = 87.2$, d.f. = 2, $P < 0.001$). The honey badger opened the tsama melons with its foreclaws 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 uses tsamas as a moisture source, in common with other carnivores and herbivores in the KTP, but they may also be important for other nutrients (Mills, 1990). 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 (February–March 1996), honey badger tracks were only located at a waterhole on one occasion.

Invertebrates: insects and scorpions

Insects were difficult to identify from visual observations and may have been underestimated. Solitary bee larvae *Parafidelia friesei* (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),

and they were ranked 13th of the 59 species for their biomass contribution. Four male honey badgers were observed digging for solitary bee larvae for 53.2 h (c. 2800 larvae) on 81 occasions, and once two male badgers were observed digging at the same larval patch at the same time. In comparison, two female honey badgers 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). Male honey badgers were therefore 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.

Excavation of a $0.6 \times 0.5 \times 1$ m block of sand within a larval patch used by honey badgers, sieved layer by layer, showed that groups of one to four larvae are found in small chambers from 13 to 100 cm below the sand surface with the highest numbers found between 50 and 70 cm. Each larva is encased in a hard brown shell c. 20 mm long, 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 11–54 holes over areas from 30 to 700 m². 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 (Begg, 2001) associated with them. Honey badgers disappeared underground when digging out these larvae, and they frequently slept in these holes after a foraging bout.

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 >10% of the diet in percentage frequency (Appendix). In terms of estimated biomass ingested they were less important (1.7% and 5%, respectively; Appendix) 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 *Rhodomys pumilio* ($n = 88$; 10%) the most commonly eaten small mammal prey species (Appendix). 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 seemed to be eaten according to their availability.

Four species, springhare *Pedetes capensis* (22.2%), mole snake *Pseudaspis cana* (21.4%), puff adder *Bitis arietans* (12.5%) and Cape cobra *Naja nivea* (10.5%), each contributed >10%, and combined 67%, of the

Table 2. An estimation of the average digging time required for the successful capture of 10 common prey items eaten by honey badgers *Mellivora capensis* in the KTP. An index of profitability is calculated as g eaten/min of digging time

Prey species	Digging time (mean \pm SE min)	Average biomass yield (g)	Index of profitability (g/digging min)
Mole snake <i>P. cana</i> ($n = 23$)	9.3 \pm 1.7	1 500	161
Cape cobra <i>N. nivea</i> ($n = 12$)	10.1 \pm 2.2	700	69.3
Horned adder <i>B. caudalis</i> ($n = 20$)	3.4 \pm 1.2	200	58.8
Brant's gerbil <i>T. brantsii</i> ($n = 145$)	3.8 \pm 0.4	64	16.8
Hairy-footed gerbil <i>G. paeba</i> ($n = 327$)	2.5 \pm 0.2	26	10.4
Giant ground gecko <i>C. angulifer</i> ($n = 101$)	2.5 \pm 0.2	23	9.2
Striped mouse <i>R. pumilio</i> ($n = 40$)	7.8 \pm 1.4	32	4.1
Barking gecko <i>P. garrulous</i> ($n = 527$)	1.3 \pm 0.04	5	3.8
Kalahari tree skink <i>M. occidentalis</i> ($n = 120$)	2.0 \pm 0.2	5	2.5
Yellow thintailed scorpion <i>O. wahlbergii</i> ($n = 167$)	2.3 \pm 0.3	5	2.2

total biomass consumed (Appendix). 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. When this female is removed from the analysis because of 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%).

Digging time and prey profitability

Prey items caught through digging, varied not only in biomass (2–2000 g) but also in digging effort. The average digging time required (min spent digging) for the successful capture of the 10 most common prey species was significantly different (Kruskal–Wallis test: $H_9 = 229.4$, $P < 0.01$, $n = 1482$; Table 2). This reflects differences in digging effort, which varied 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 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).

Calculation of a coarse estimate of the profitability of these 10 most common prey species (biomass consumed (g) per min of digging time), showed that the large snakes, particularly the non-venomous mole snake (*P. cana*) were the most profitable prey species and were four to 10 times more profitable than the two common small mammals (hairy footed gerbil and Brant's gerbil; Table 2).

The largest prey species caught by a honey badger in the KTP during the study was the springhare (2000 g). As noted above, 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 probably have similarly high profitability indexes. Since visual observations of the capture of these prey items were rare, this precluded further analysis.

Seasonal variation in diet

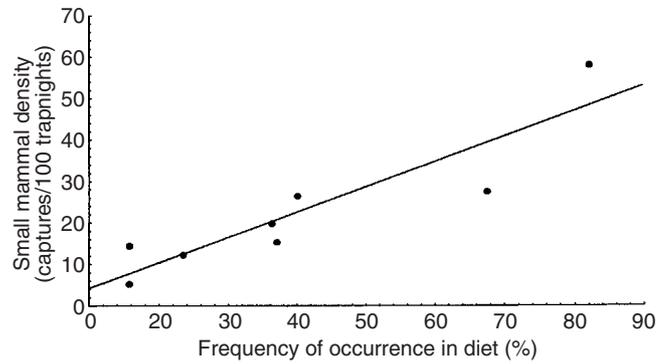
Both Levin's measure of niche breadth and the Brillouin index were highest in the hot-wet season and lowest in the hot-dry season, with the cold-dry season intermediate (Table 3). In contrast, the species richness of the diet in the hot-dry season was more than twice that of the cold-dry season, with the hot-wet season intermediate at 35 prey species (Table 3). While the consumption of small mammals and birds showed no significant seasonal variation (Chi-square test, small mammals: $\chi^2 = 1.1$, d.f. = 2, NS; birds: $\chi^2 = 3.4$, d.f. = 2, NS), there were significant seasonal

Table 3. Seasonal differences in the diversity (Levin's niche breadth index and Brillouin index) and species richness of the diet of honey badgers *Mellivora capensis* 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

differences in the frequency of prey consumed in all the other food categories, particularly scorpions and large reptiles (Chi-square test, insects: $\chi^2 = 17.2$, d.f. = 2, $P < 0.01$; solitary bee larvae: $\chi^2 = 81.9$, d.f. = 2, $P < 0.01$; scorpions: $\chi^2 = 60.4$, d.f. = 2, $P < 0.001$; large reptiles: $\chi^2 = 99.5$, d.f. = 2, $P < 0.001$; small reptiles: $\chi^2 = 28.2$, d.f. = 2, $P < 0.001$; large mammals: $\chi^2 = 27.3$, d.f. = 2, $P < 0.001$; Table 4). Small mammals (<100 g) and small reptiles (<100 g) were the most common prey items and together contributed >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 4). 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 4% in the hot-wet season (Table 4). 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 4).

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. arietans*, Cape cobra *N. nivea*), they contributed 58% of the biomass consumed in this season. While snakes did

**Fig. 1.** The relationship between percentage frequency of small mammals consumed by honey badgers *Mellivora capensis* and the relative abundance of small mammals estimated from rodent trapping from the cold-dry season 1997 to the hot-dry season 1999.

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 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 >5% of prey biomass in any season (Table 4).

Annual changes

When data were analysed 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 ($n = 8$, $r_s = 0.89$, $P < 0.01$; Fig. 1). Both small reptile and scorpion consumption were

Table 4. 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 category	Prey consumed					
	% Frequency			% 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	0	0	0.1
Solitary bee larvae ^a	6.7	0.8	0.7	8.5	0.5	0.1
Scorpions	12.4	3.7	6.7	2.6	0.2	0.3
Small reptiles (<100g)	41.0	49.6	32.7	10.8	3.6	1.1
Large reptiles (>100 g)	1.4	5.4	13.8	25.1	41.2	58.4
Small mammals (<100 g)	37.6	36.2	39.3	39.4	14.9	3.9
Large mammals (>100 g)	0.3	2.0	3.8	12.1	36.1	35.4
Birds	0.7	1.5	1	1.6	3.5	0.8

^a 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.

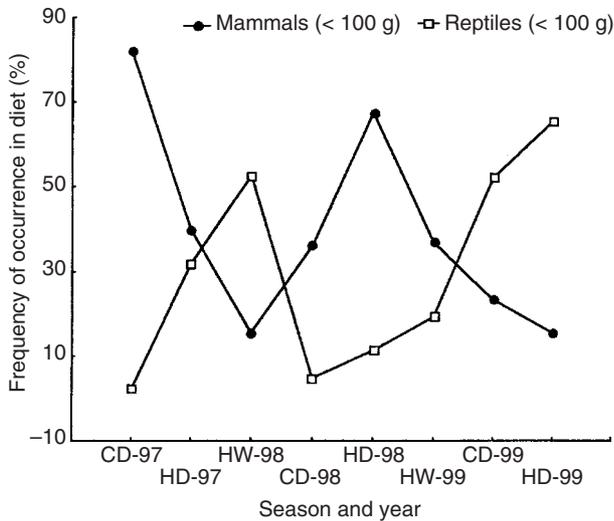


Fig. 2. Annual and seasonal changes in the proportions of small reptiles, scorpions and small mammals in the diet of honey badgers *Mellivora capensis* in the KTP from visual observations.

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 (Fig. 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 (Figs 2 & 3). Tsama melons and solitary bee larvae (Fig. 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 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 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 (Fig. 4), solitary bee larvae were no longer eaten and assumed to be no longer available (Fig. 5), 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

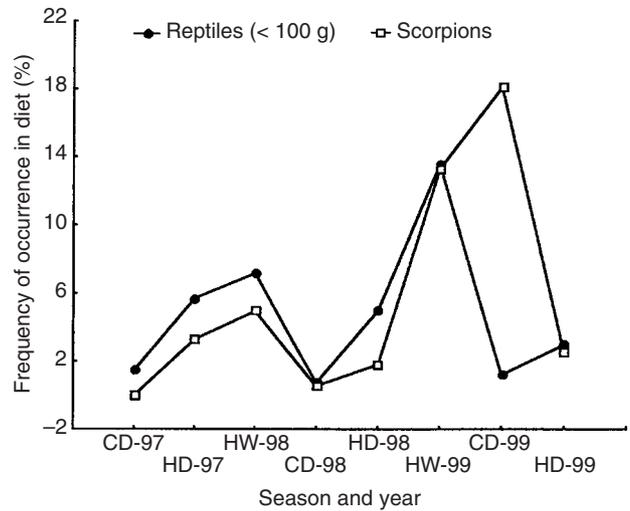


Fig. 3. Seasonal and annual changes in the frequency of occurrence of scorpions and large reptiles in the diet of honey badgers *Mellivora capensis* in the KTP from visual observations.

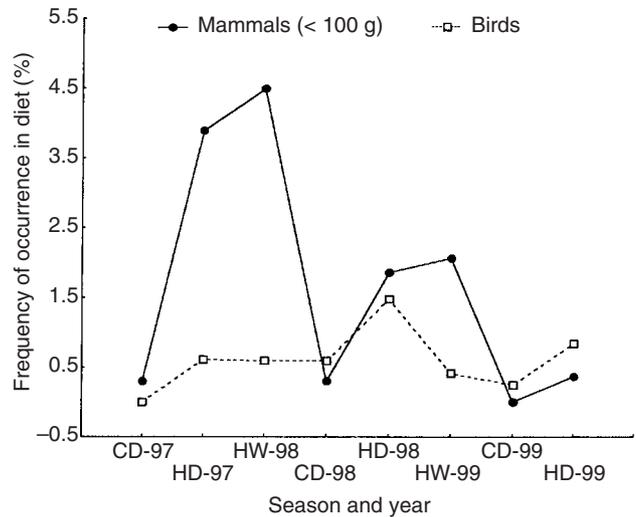


Fig. 4. Seasonal and annual changes in the frequency of occurrence of large mammals and birds in the diet of honey badgers *Mellivora capensis* in the KTP.

to death during this period (confirmed by a post mortem examination done by Dr D. Grobler, Kruger National Park veterinarian).

Sexual differences in body size, diet and foraging behaviour

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 (two-tailed t -test: $t = 7.49$, d.f. = 26, $P < 0.001$; Table 5), shoulder height (two-tailed

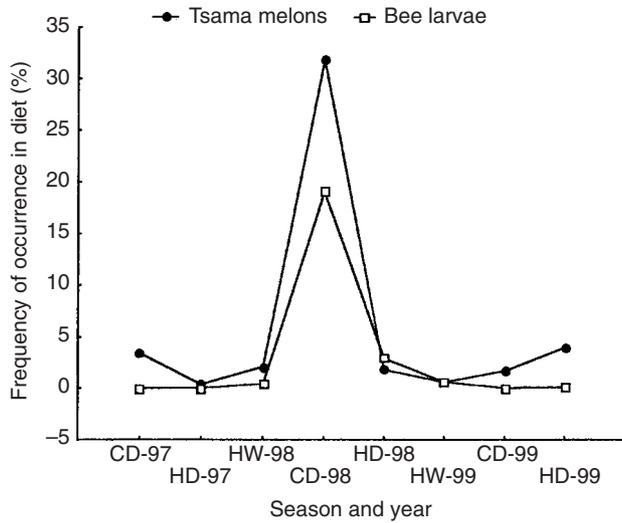


Fig. 5. Seasonal and annual changes in the frequency of occurrence of tsama melons and solitary bee larvae in the diet of honey badgers *Mellivora capensis* in the KTP, showing the peak in the diet in the cold-dry season of 1998 in both food categories.

t-test: $t = 7.81$, d.f. = 26, $P < 0.001$; Table 5) and mass (two-tailed *t*-test: $t = 10.82$, d.f. = 28, $P < 0.001$; Table 5). At the age of 6–8 months male and female cubs are already sexually size dimorphic (Fig. 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.

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 6). Larger reptiles (>100 g), made up exclusively of large snakes, were the largest contributors of biomass (females 46%; males 53%) with larger mammals (>500 g), contributing >30% in female diets

Table 5. Mean and standard error of linear and mass measurements of male and female adult honey badgers *Mellivora capensis* in the KTP

Measurement	♀ Overall (n = 13)	♂ Overall (n = 17)
	Mean (SE)	Mean (SE)
Mass (kg)	6.2 (0.14)	9.4 (0.23)
Body length (mm)	636 (11.4)	724 (5.83)
Shoulder height (mm)	352 (4.37)	397 (3.73)

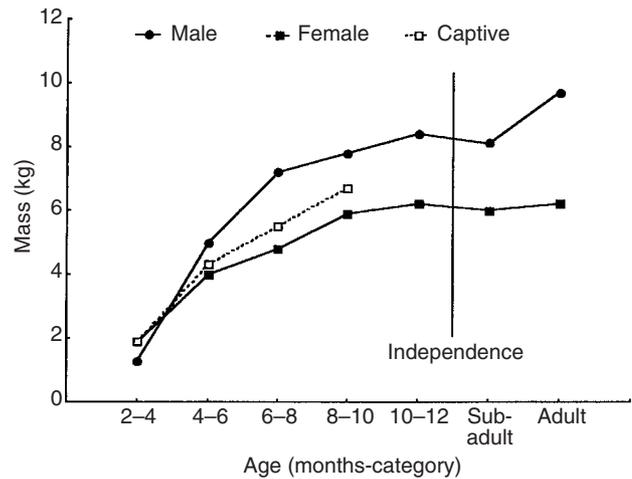


Fig. 6. Average mass of male and female honey badger *Mellivora capensis* cubs of different ages captured during the study. Data on the mass increase of a female cub hand-reared in Howletts Zoo, UK, is also shown for comparison (adapted from Johnstone-Scott, 1975).

and 23% in male diets, and ranked second in importance (Table 6).

There were no intersexual differences in the rank order of biomass consumed in the top five prey categories (Table 6), and overall species richness and niche breadth were similar in both sexes (Table 6). Seasonally, females and males also showed a similar pattern in prey diversity

Table 6. Sexual differences in the diet of habituated honey badgers *Mellivora capensis* (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

Prey category	♀ Diet (n = 1658)				♂ Diet (n = 1024)			
	% Frequency	Rank	% Biomass	Rank	% Frequency	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			

with the highest value for the niche breadth index in the hot-wet season (3.3 and 4.1), and similar lower values in the cold-dry (2.3 and 2.6) and hot-dry season (2.3 and 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, both male and female honey badgers took prey ranging from 2 to 2000 g and there were no significant differences in the number of large (>100 g; 8.6% vs 7.3%), medium (5–100 g; 79.4% vs 82.9%) or small (<5 g; 12% vs 9.8%) sized prey taken by female ($n = 1658$ prey items) and male badgers ($n = 1024$ prey items) respectively (chi-square test: $\chi^2 = 4.97$, d.f. = 2, NS).

Foraging behaviour

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 upwind 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 used 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; Begg, 2001). Whilst engaged in these social activities, males caught 9.8% of their prey biomass opportunistically.

There were significant intersexual differences in the method of prey capture (chi-square test: $\chi^2 = 49.5$, d.f. = 2, $P < 0.001$). Post-hoc investigation shows that while both sexes catch the majority of prey through digging (females: 85%; males: 80%), with similar percentages of prey caught above ground (females: 12%; males: 11%; chi-square test: $\chi^2 = 2.9$, d.f. = 3, NS), the differences lie in the amount of prey caught through climbing and ripping off bark and climbing (3% vs 9%). 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 the tail and 'padding' 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 honey badgers were never seen

Table 7. The average daily consumption of male and female honey badgers *Mellivora capensis* determined from continuous 24 h observation periods and expressed as the mean (SE) biomass of food eaten per day and the biomass ingested per kg 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) mean \pm SE	Consumption (kg/kg bodyweight per day)
♂ Overall ($n = 64$)	9.4 (0.94)	1.3 \pm 0.15	0.1 \pm 0.01
♀ Overall ($n = 67$)	6.2 (0.52)	0.9 \pm 0.11	0.2 \pm 0.02
♂ HB12 ($n = 28$)	11	1.0 \pm 0.27	0.1 \pm 0.03
♀ HB38 ($n = 30$)	6	0.7 \pm 0.19	0.1 \pm 0.03

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).

Rate of food intake, digging success, time spent foraging

Honey badgers foraged every day even when the previous day's foraging had been successful. No significant individual differences in daily consumption were observed within adult females (Kruskal–Wallis test: $H_4 = 7.7$, NS, $n = 67$) or adult males (Kruskal–Wallis test: $H_3 = 1.6$, NS, $n = 64$). Overall (data pooled for each sex) males consumed significantly more food per day than females (two-sample t -test: $t = -2.57$, d.f. = 129, $P < 0.05$, Table 7). However, there was no significant difference in the mean percentage of their body weight consumed per day (two-sample t -test: $t = 0.528$, d.f. = 129, NS; Table 7). On one occasion a male badger (HB12), weighing 11 kg, consumed at least 6.6 kg of meat in 1 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. A direct comparison between two adult middle-aged honey badgers, one male (Am12) and one female (Am38), of known body weight was made. The home range of the female lay within the home range of the male, and they used similar habitat over a similar time period (1998–99). The same result was obtained, with both the male and the female ingesting 0.1 kg of food/kg of body mass/day (Table 7).

While males and females without cubs consumed all the food that was caught (i.e. foraging rate = consumption rate; Table 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 (Begg, 2001) 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% (SE = 6.6, $n = 16$ observation periods) of the food biomass caught by a female during a foraging period, and this increased to 45% (SE = 2.7, $n = 66$

Table 8. Comparison of consumption rate, foraging rate and digging success of male and female honey badgers *Mellivora capensis* 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

	Females		Males	Significance test
	♀ No cubs mean (SE; <i>n</i>)	♀ Dependent cubs mean (SE; <i>n</i>)	♂ Overall mean (SE; <i>n</i>)	
Hunting behaviour				
Consumption rate (g eaten/foraging min.)	4.9 (1.0; 45)	3.4 (0.5; 76)	2.6 (0.4; 167)	Kruskal–Wallis $H_2 = 8.06$ $P < 0.05$
Foraging rate (g caught/foraging min.)	4.9 (1.0; 45)	5.9 (0.8; 76)	2.6 (0.4; 167)	Kruskal–Wallis $H_2 = 21.9$ $P < 0.05$
Digging success ^{a,b} (%)	40 (2.1; 45)	41.6 (2.6; 76)	49 (2.2; 167)	ANOVA $F_{2,288} = 1.5$ NS

^a Proportions were arcsine transformed to normalize for ANOVA analysis, then backtransformed for means (Zar, 1999).

^b 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 one to six holes dug for a single prey item.

observation periods) from 6 months until independence. The consumption rate of females tended to decrease when they had dependent cubs compared to when they foraged alone (two-sample *t*-test: $t = -1.62$, d.f. = 119, NS), while the foraging rate tended to increase (two-sample *t*-test: $t = 0.59$, d.f. = 119, NS), although these differences were not significant (Table 8). Overall females, both with and without cubs, had a significantly higher consumption rate and foraging rate than males (Table 8).

Seasonally, there were no significant differences in the biomass ingested per kg of body weight in either males or females (Table 9). 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 9). In addition, female honey badgers showed significantly higher digging success in the cold-dry season, with the same trend in the males (Table 9).

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 seemed 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 seem to reflect changes in food availability. Similar seasonal shifts in diet have been documented in

a variety of north temperate mustelid species (Zielinski, Spencer & Barrett, 1983; Dunstone, 1993; Lode, 1994; Genovesi, Secchi & Boitani, 1996; Martinoli *et al.*, 2001). Small mammals are the staple prey of honey badgers, 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 seem 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 (Steyn, 1982; Skinner & Smithers, 1990). While no data were collected on the variation in actual abundance of other prey categories during this study, small reptile populations seem to be highest in late summer (hot-wet season; W. Haacke, pers. comm.), while scorpions (L. Prendini, pers. comm.) and large reptiles (B. Branch, pers. comm.) are unlikely to vary in their actual abundance in the short term (monthly) because of their long lifespans 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, pers. comm.). During the hot-dry season there is increased snake and small reptile activity as a result of 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 probably reduced (increased search time)

Table 9. Seasonal variation in consumption rate, hunting success and biomass ingested per g of body weight of honey badgers in the KTP

Foraging behaviour	Females mean (SE; n)				Males mean (SE; n)				Significance test
	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 $H_2 = 13.4$ $P < 0.05$	5.7 (1.1; 26)	1.3 (0.3; 71)	3.5 (0.6; 70)	Kruskal-Wallis $H_2 = 13.63$ $P < 0.05$	
Digging success ^{a,b}	32.3 (2.4; 55)	41.7 (1.9; 39)	37.8 (3.6.9; 82)	ANOVA $F_{2,179} = 4.85$ $P < 0.05$	36.0 (3.9; 26)	39.7 (1.9; 71)	39.1 (1.7; 70)	ANOVA $F_{2,164} = 0.23$ NS	
g ingested/kg of body mass per day	0.2 (0.03; 24)	0.1 (0.05; 10)	0.1 (0.02; 33)	Kruskal-Wallis $H_2 = 0.05$ NS	0.1 (0.03; 10)	0.1 (0.02; 24)	0.2 (0.03; 27)	Kruskal-Wallis $H_2 = 0.12$ NS	

^a Proportions were arcsine transformed to normalize for ANOVA analysis, back transformed to calculate means (Zar, 1999).

^b 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 one to six holes dug for a single prey item.

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 true.

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 were eaten and the consumption rate was 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 1.4 g/min in the cold-dry season, it is probable that cubs also obtain proportionally less food during these months. The starvation of a young 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.

Yet, the honey badger seems to be unusual amongst the mustelids (Johnson, Macdonald & Dickman, 2000), as it does not have a distinct breeding season in the KTP (Begg, 2001). The lack of a breeding season may be a consequence of the long cub dependency (14–18 months), which results in a birth interval of > 12 months (Kruuk, 1995). However, other sources have suggested that breeding is seasonal in other parts of its range, i.e. spring births and autumn matings in Turkmenia, USSR and births timed to coincide with the maximum availability of honey in Central Africa and Nigeria (Kingdon, 1989). Given the lack of studies on the honey badger in other areas, this could not be confirmed.

The hot-dry and hot-wet season seem 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 (g/foraging min) 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 & 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 seem 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 (Begg, 2001). Unfortunately no data are available on associated 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 *Meles meles*) to 2.24 (weasel *Mustela nivalis*), with extreme dimorphism defined as a value >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 (1.15; Moors, 1980) and the North American badger (1.2; Messick & Hornocker, 1981).

In support of the hypothesis that sexual size dimorphism reduced intersexual resource competition, preliminary data collected in the same habitat in the KTP by Kruuk & Mills (1983) suggested that male and female honey badgers use different foraging strategies, with females 'short-distance foragers' covering an average of 5 km/day, catching predominantly small prey, while males are 'long-distance foragers' covering an average distance of 27 km/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 (Begg, 2001), $<10\%$ 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; Begg, 2001) 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 for biomass, in both sexes, in the same order. These significant differences in frequency may be the result of 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. The reasons for these sexual differences in the consumption of solitary bee larvae are unknown.

Alternatively, these differences might be a consequence of sexual differences in the spatial organization of honey badgers (Begg, 2001), 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 for solitary bee larvae and breeding birds, seem to be patchily distributed. It is possible that since females forage intensively over the same ground daily (Begg, 2001), their encounter rates of patchy prey items are reduced in times of low abundance due to prior exploitation or reduced distribution. They might then use 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 (Moors, 1980; Erlinge, 1981), there is no evidence that the smaller female honey badgers take smaller prey than males. Both sexes kill prey ranging in mass from 1 g (insect larvae) to 2000 g (springhares). In addition, there are no sexual differences in digging success or in the digging effort required to catch any of 10 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 use 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 that males are larger than females. To meet their energetic demands, males forage for 5–6% longer than females each day (Begg, 2001) and catch food opportunistically during social activities, and this counters their low consumption rate. Although females are expected to have higher energetic demands resulting from pregnancy, lactation and cub rearing (Ofstedal & 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 too are social activities such as scent marking and long-distance walking in males (Begg, 2001). 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 (Begg, 2001), rather than bioenergetics (Lups & Roper, 1988).

Acknowledgements

This research was supported by the Carnivore Conservation Group of the Endangered Wildlife Trust, South Africa, The University of Pretoria and the National Research Foundation of South Africa. MGLM is supported by the Tony and Lisette Lewis Foundation. We thank South African National Parks for permission to do the study in the Kgalagadi Transfrontier Park and for aerial tracking support and Drs Douw Grobler, Pete Morkel, Mike Kock and Erick Verrenne for veterinary assistance. We remain indebted to the late Klaas Kruiper for finding and interpreting the tracks of honey badgers and we thank Martyn Gorman, Jon Swenson and two anonymous referees for critical comments on this manuscript.

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

Prey item	Overall			♀		♂	
	No. eaten	Biomass (g) eaten	% Total biomass	No. eaten	% Total biomass	No. eaten	% Total biomass
Springhare <i>Pedetes capensis</i>	28	56000	22.19	26	32.71	2	4.25
Mole snake <i>Pseudaspis cana</i>	36	54000	21.39	20	18.87	16	25.52
Puff adder <i>Bitis arietans</i>	21	31500	12.48	12	11.32	9	14.36
Cape cobra <i>Naja nivea</i>	38	26600	10.54	27	11.89	11	8.19
Brants gerbil <i>Tatera brantsii</i>	218	14170	5.61	170	6.95	48	3.32
Hairy-footed gerbil <i>Gerbillurus paeba</i>	480	12480	4.94	235	3.84	245	6.77
African wild cat <i>Felis lybica</i> (1 adult, 1 kitten)	2	6000	2.38	0	0.00	2	6.38
Horned adder <i>Bitis caudalis</i>	22	4400	1.74	11	1.38	11	2.34
Common barking gecko <i>Ptenopus garrulous</i>	845	4225	1.67	631	1.98	214	1.14
Cape fox <i>Vulpes chama (cubs)</i>	5	4000	1.58	1	0.50	4	3.40
Scrub hare <i>Lepus saxatilis</i>	2	4000	1.58	0	0.00	2	4.25
Yellow mongoose <i>Cynictis penicillata</i>	6	3480	1.38	4	1.82	2	1.23
Solitary bee larvae <i>Parafidelia friesei</i> ^a	84	2983 ^c	1.18	3	0.1	81	3.17
Striped mouse <i>Rhabdomys pumilio</i>	88	2816	1.12	26	0.52	62	2.11
Sand snakes <i>Psammodphis</i> sp.	14	2800	1.11	11	1.38	3	0.64
Giant ground gecko <i>Chondrodactylus angulifer</i>	111	2553	1.01	78	1.13	33	0.81
Pale chanting goshawk <i>Melierax canorus</i> (chicks)	5	2500	0.99	0	0.00	5	2.66
Kalahari tree skink <i>Mabuya occidentalis</i>	198	1980	0.83	8	0.88	190	0.74
Striped polecat <i>Ictonyx striatus</i>	3	2100	0.78	2	0.05	1	2.02
Black korhaan <i>Eupodotis afra</i>	3	1800	0.71	2	0.75	1	0.64
Bat-eared fox <i>Otocyon megalotis (ISA, 1cub)</i>	2	1600	0.63	1	0.50	1	0.85
Suricate <i>Suricata suricatta</i>	2	1400	0.55	1	0.44	1	0.74
Honey badger (cub) <i>Mellivora capensis</i>	2	1000	0.40	0	0.00	2	1.06
Yellow scorpion <i>Opisththalmus wahlbergii</i>	190	950	0.38	177	0.56	13	0.07
Bibrons stiletto <i>Atractaspis bibronii</i>	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 <i>Parotomys brantsii</i>	9	720	0.29	8	0.40	1	0.09
Bicoloured quill-snouted snake <i>Xenocalamus bicolor bicolor</i>	3	600	0.24	3	0.38	0	0.00
Namaqua sandgrouse <i>Pterocles namaqua</i>	2	600	0.24	1	0.19	1	0.32
Spotted eagle owl <i>Bubo africanus</i> (chick)	2	600	0.24	1	0.19	1	0.32
Ant eating chat <i>Myrmecocichla formicivora</i>	12	480	0.19	9	0.23	3	0.13
Cape gecko <i>Pachydactylus bibronii</i>	27	351	0.14	19	0.16	8	0.11
Barn owl <i>Tyto alba</i>	1	300	0.12	0	0.00	1	0.32
Bushveld elephant shrew <i>Elephantulus intufi</i>	5	210	0.08	4	0.11	1	0.04
Short-tailed gerbil <i>Desmodillus auricularis</i>	4	184	0.07	0	0.00	4	0.20
Spotted eagle owl eggs	3	135	0.06	0	0.00	3	0.16

Appendix. Continued

Prey item	Overall			♀		♂	
	No. eaten	Biomass (g) eaten	% Total biomass	No. eaten	% Total biomass	No. eaten	% Total biomass
African rock python (juvenile) <i>Python sebae natalensis</i>	1	150	0.06	0	0.00	1	0.16
Common quail <i>Coturnix coturnix</i>	1	95	0.04	1	0.06	0	0.00
Termites (alates) <i>Hodotermes mossambicus</i> (34 individuals) ^a	1	68	0.03	1	0.02	0	0.00
Beetle: Scarabaeidae; subfamily: Melolonthinae (31 individuals) ^a	4	62	0.02	1	0.00	3	0.06
Pygmy mouse <i>Mus minutoides</i>	12	60	0.02	5	0.02	7	0.04
Yellow scorpion <i>Parabuthus raudus</i>	9	45	0.02	4	0.01	5	0.03
Striped sandveld lizard <i>Nucras t. tessellata</i>	4	60	0.02	3	0.03	1	0.02
Ground agama <i>Agama aculeate</i>	2	50	0.02	2	0.03	0	0.00
Lark sp.	1	60	0.02	0	0.00	1	0.06
Pouched mouse <i>Saccostomus campestris</i>	1	47	0.02	0	0.00	1	0.05
Woosnams desert rat <i>Zelotomys woosnami</i>	1	62	0.02	1	0.04	0	0.00
Maggots Order: Diptera (8 individuals) ^a	1	16	0.01	1	0.01	0	0.00
Black scorpion <i>Opisthophthalmus carinatus</i>	5	25	0.01	4	0.00	1	0.00
Black/brown scorpion <i>Parabuthus granulatus or kalaharicus</i> ^b	3	15	0.01	0	0.00	3	0.02
Black and yellow sand lizard <i>Heliobolus lugubris</i>	2	20	0.01	2	0.01	0	0.00
Scaly feathered finch <i>Sporopines squamifrons</i>	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 <i>Philetairus socius</i> ^a	3	—	—	0	—	3	—
Owl pellet ^d	2	—	—	0	—	2	—
Snake skin ^d	2	—	—	0	—	2	—
Total	2550	249405		1526		1024	

^a Number eaten represents feeding events not individuals.

^b Identification of scorpion remains in scats (Lorenzo 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*.

^c Biomass estimated from time spent feeding at 0.88 larvae/min.

^d Prey items assumed to have little biomass value.