- 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
Large				
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 ($\bar{x} = 1$). Jackals were observed with habituated honey badgers for 236 h comprising 156 observation periods ranging in duration from 2 – 847 min ($\bar{x} = 110$ 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 ($\bar{x} = 385$ min), waiting for the honey badger to emerge for the next foraging bout.

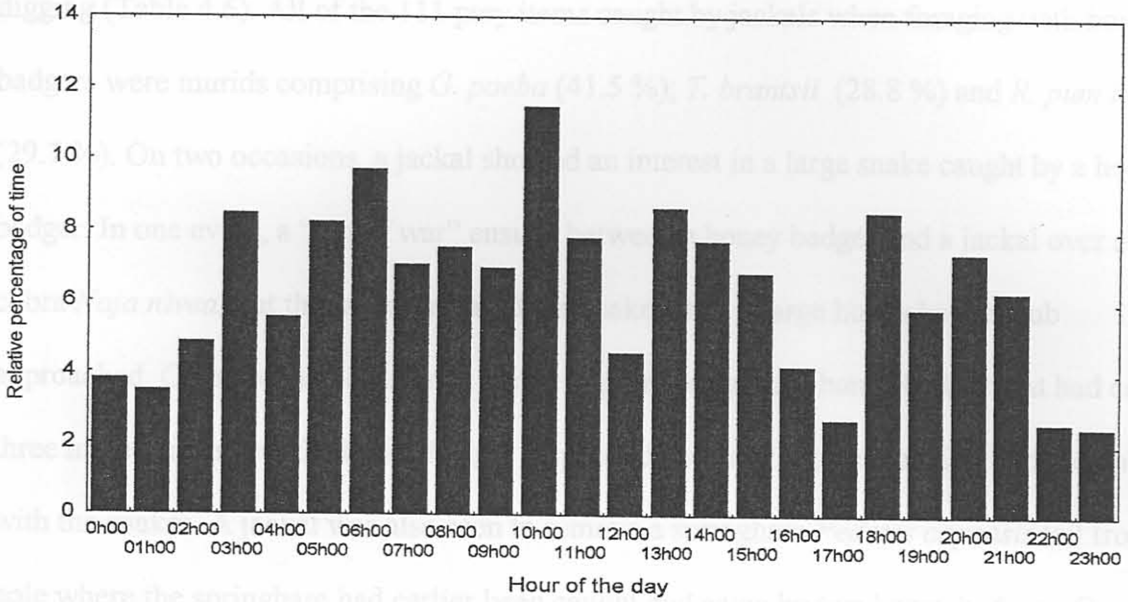

Figure 4.1 Percentage of time black-backed jackals were observed with honey badgers, relative to the number of hours honey badgers were observed foraging during each hour of the day, averaged over the study period (1996-1999).

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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