- Chapter 3 -

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

3.1 Abstract

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

3.2 Introduction

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

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

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

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

3.3 Methods

3.3.1 Study area

The project was initiated in July 1996 and continued until December 1999 (42 months) in the Kgalagadi Transfrontier Park (KTP), which encompasses an area of 36 200 km^2 with the Kalahari Gemsbok National Park, South Africa and neighbouring Gemsbok National Park, Botswana.

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

3.3.2 Climate

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

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

3.3.3 Study population

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

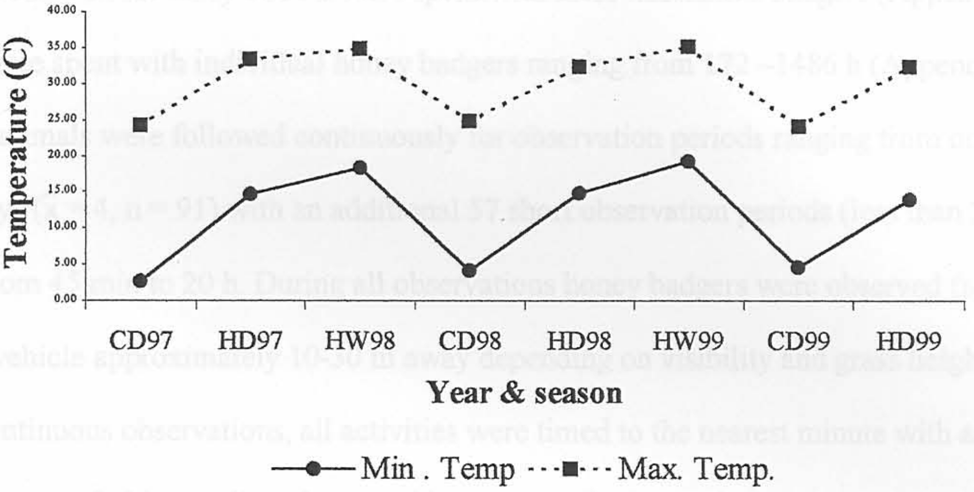


Figure 3.1 Seasonal changes in the average maximum and minimum temperatures during the study period in the KTP.

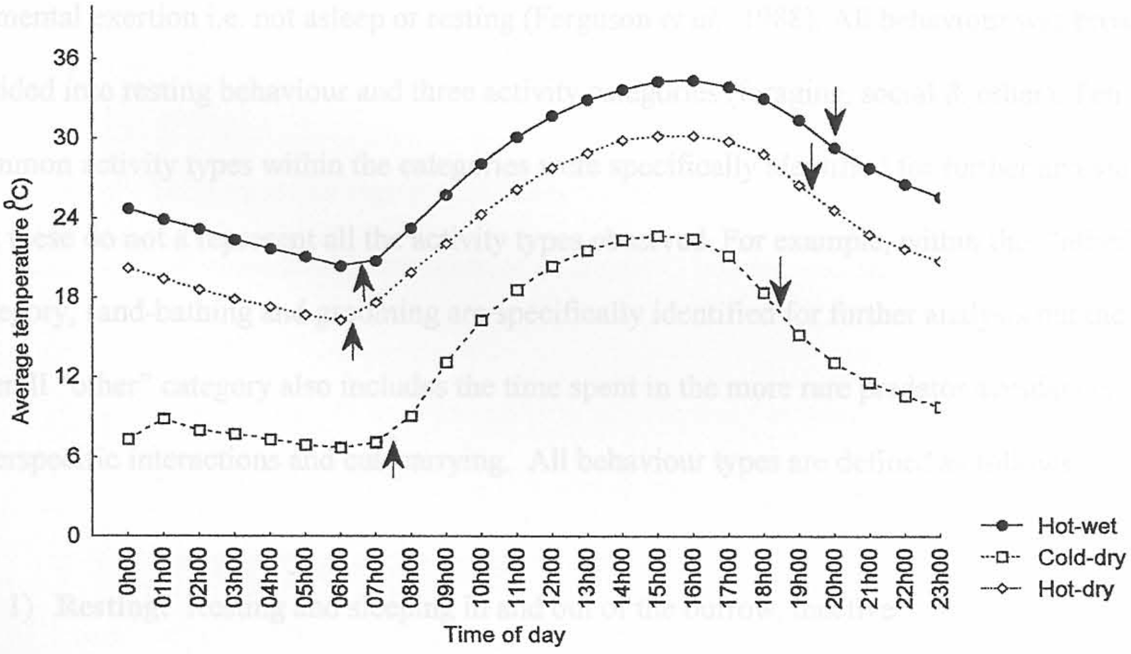


Figure 3.2 Average hourly changes in temperature in the hot-wet, cold-dry and hot-dry season calculated from the nearest town, Upington (provided by the South African Weather Bureau). The arrows indicate the average time of sunrise and sunset for each season calculated from a GPS location in the centre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

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

3.3.4 Definition of terms

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

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

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

3.3.4 Data analysis

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

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

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

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

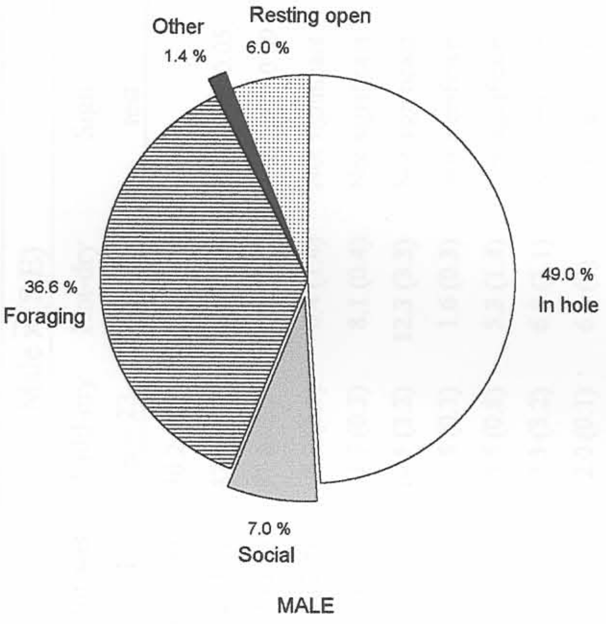
3.4 Results

3.4.1. Time budgets

3.4.1.1 Sexual differences

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

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



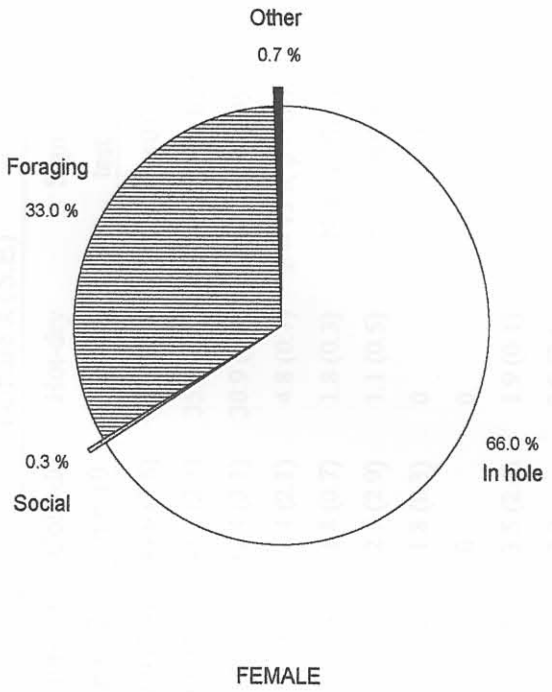


Figure 3.3 Overall sexual differences in the daily time budgets of the honey badger calculated from continuous 24 h observations of habituated individuals (Males: n = 61 days; females: n = 63 days). Social behaviour refers to latrine checking, scent marking, and intraspecific interactions while "other"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

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

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

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

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

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

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

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

3.4.1.2 Seasonal differences

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

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

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

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

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

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

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

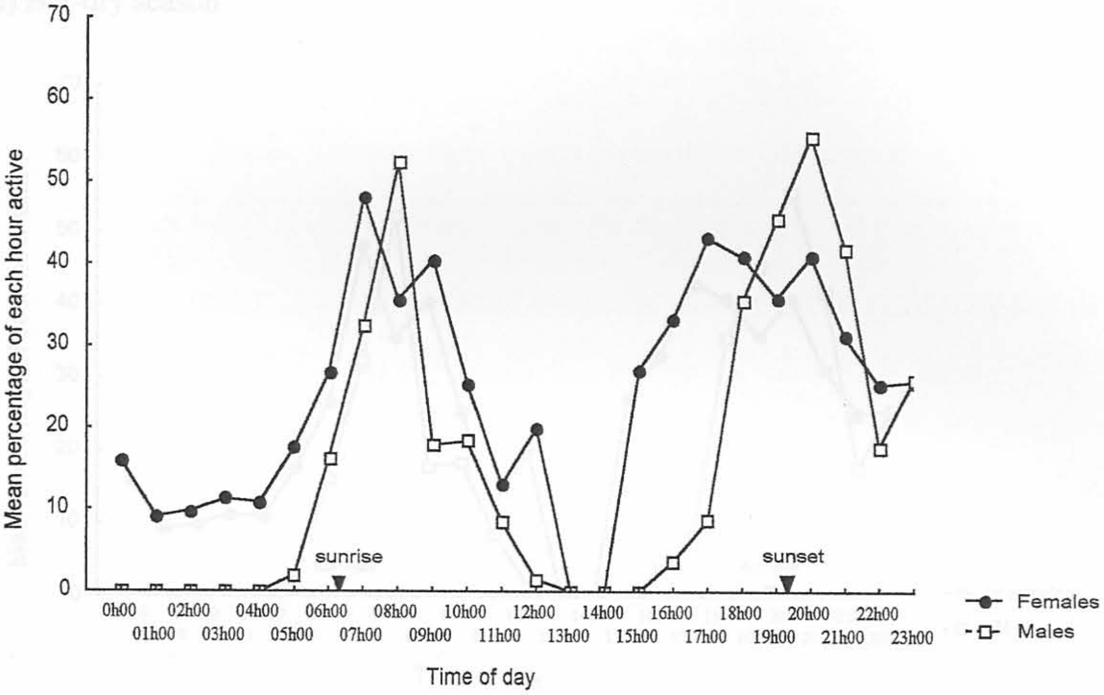
3.4.2. Activity patterns

<u>3.4.2.1 Active periods</u>

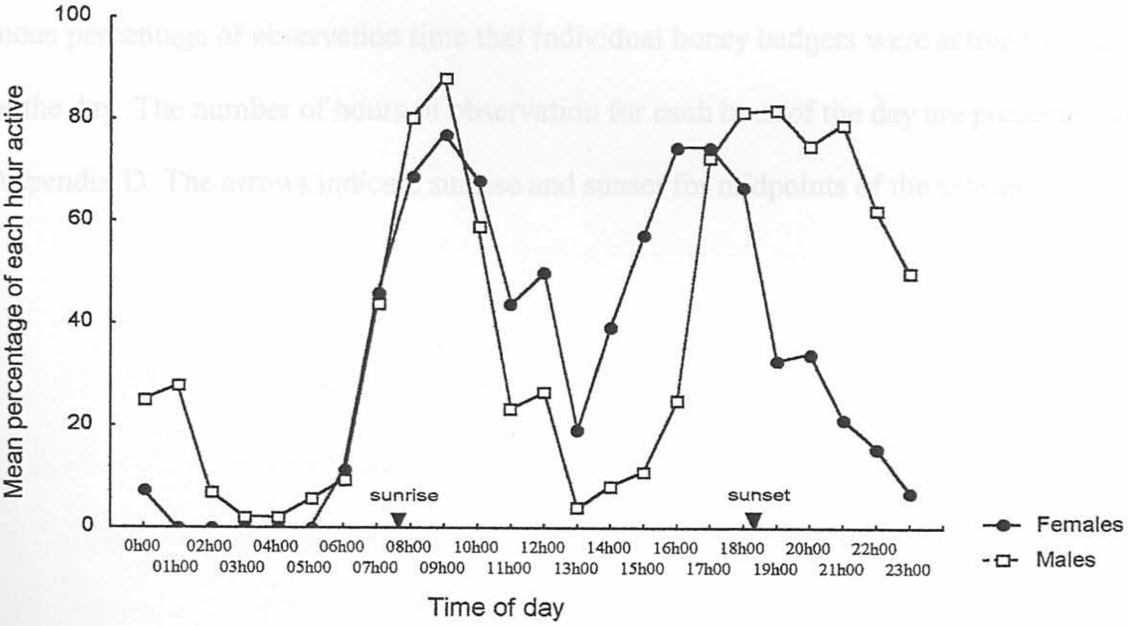
Male and female honey badgers showed a similar bigeminus (two peaked; Aschoff, 1966) activity pattern with the two daily peaks in activity in the morning and evening and a sharp decline in activity during the middle of the day in all seasons, but particularly during the hot-dry and hot-wet season (Figure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

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

a) Hot-wet season



b) Cold-dry season



c) Hot-dry season

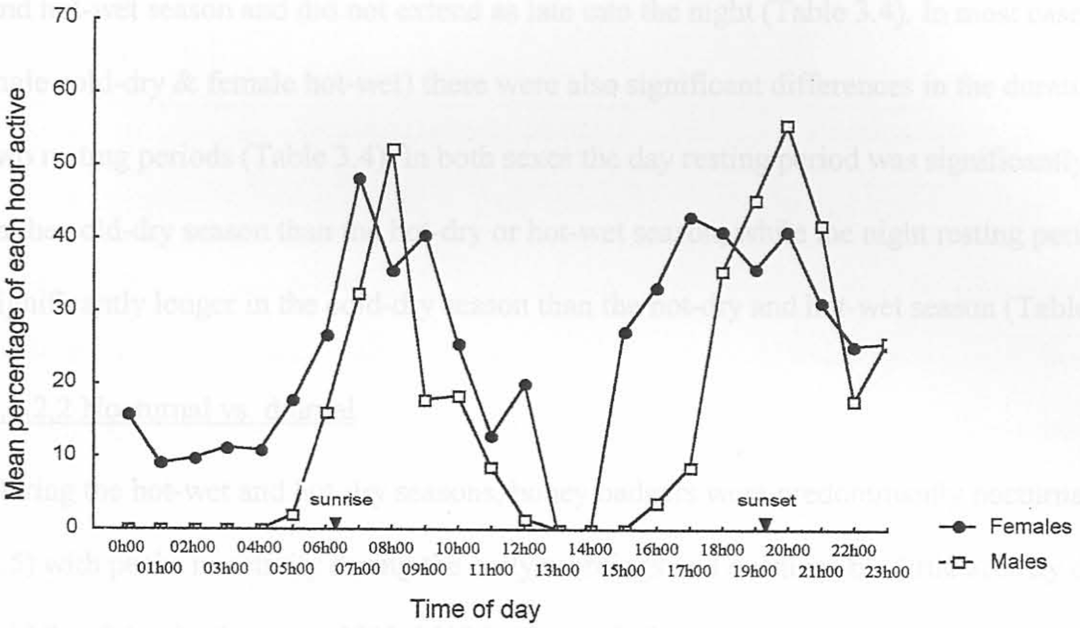


Figure 3.4 Daily activity schedule of male and female honey badgers in the hot-wet (a), cold-dry (b) and hot-dry (c) season showing the two-peaked pattern. Data were calculated as the mean percentage of observation time that individual honey badgers were active for each hour of the day. The number of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

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

3.4.2.2 Nocturnal vs. diurnal

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

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

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

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

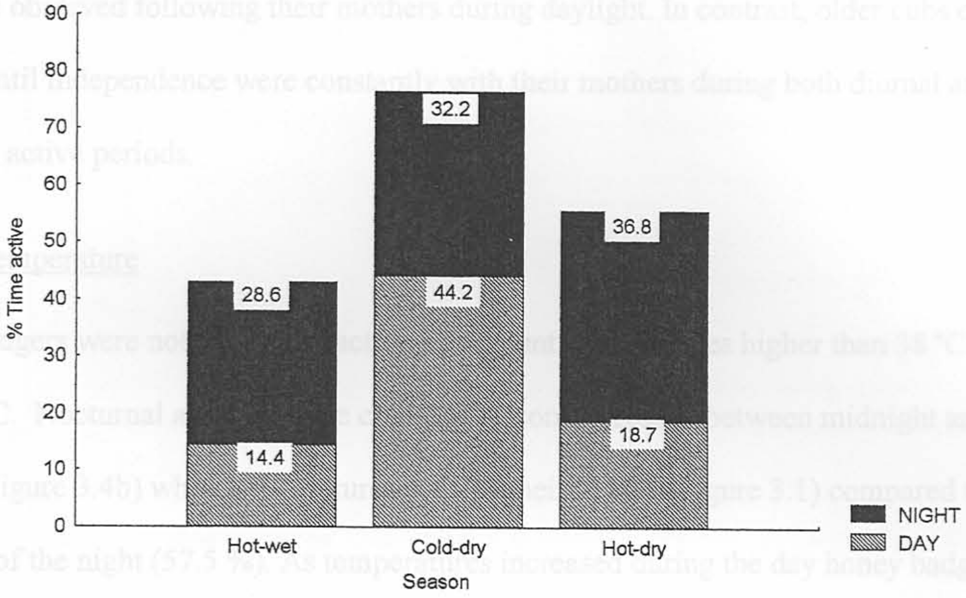


Figure 3.5 Seasonal differences in the relative nocturnal and diurnal activity of honey badgers in the KTP. To account for different amounts of observation time during the day and night, the time spent active was calculated as a percentage of the amount of time a honey badger were observed in each period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

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

3.4.2.3 Temperature

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

3.4.2.4 Prey activity

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

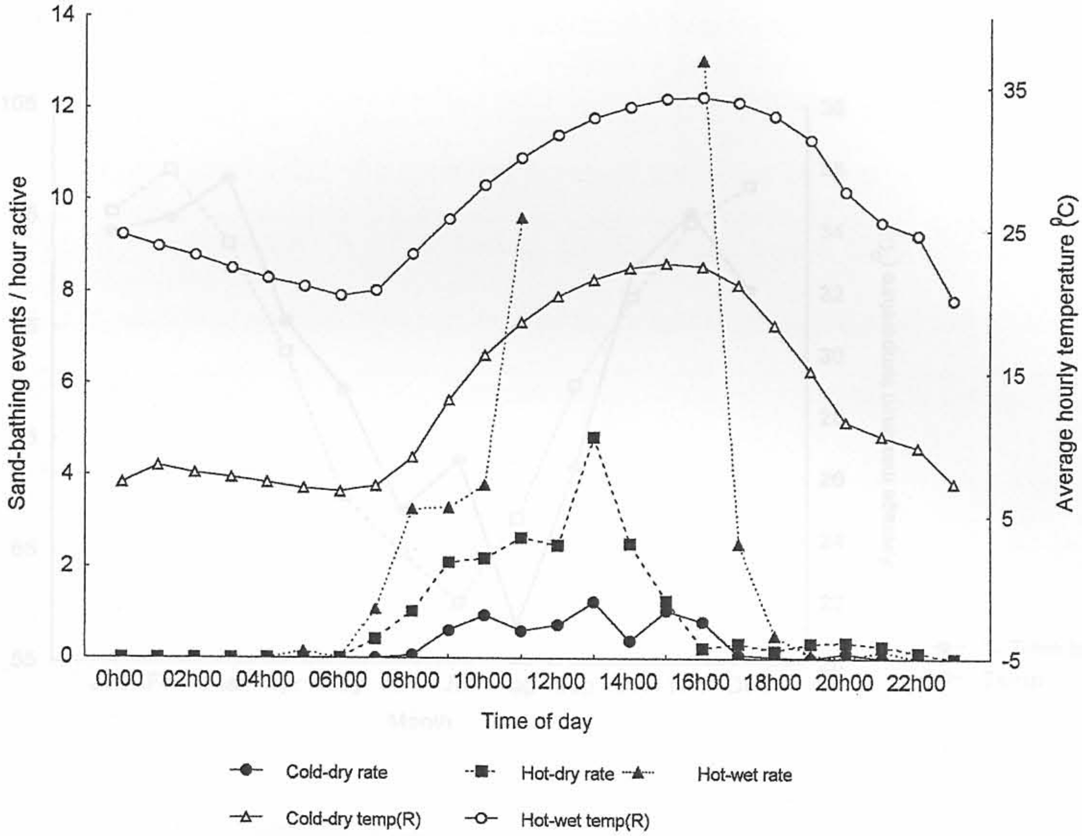


Figure 3.6 The frequency of sand-bathing events in honey badgers in the KTP and hourly changes in maximum temperature in the cold-dry and hot-wet season. Sand bathing frequency was calculated as the number of sand bathing events observed per hour of activity recorded for that hour of the day. The disjunction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

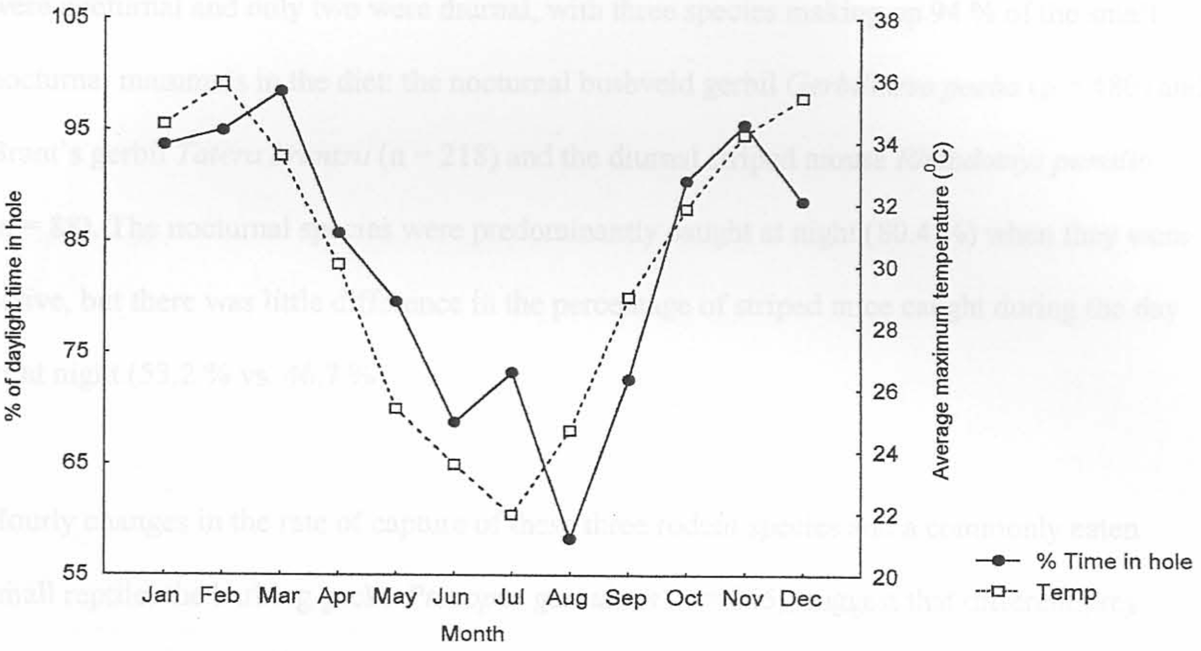


Figure 3.7 Relationship between average maximum temperature and the percentage of time honey badgers rest in a burrow during the daylight hours showing the increase in burrow use with increasing temperature. Spearmans rank correlation, $r_s = 0.79$, $p = 0.002$.

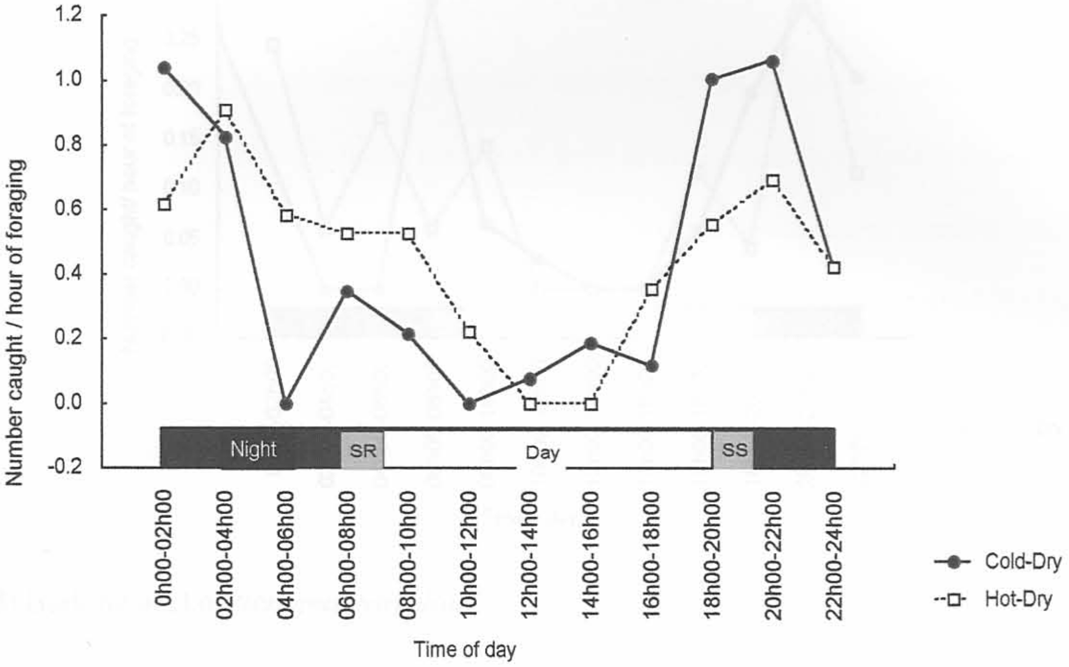
(Table 3.6). Of the nine small mammal species eaten by honey badgers in the KTP, seven were nocturnal and only two were diurnal, with three species making up 94 % of the small nocturnal mammals in the diet: the nocturnal bushveld gerbil *Gerbillurus paeba* (n = 480) and Brant's gerbil *Tatera brantsii*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

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

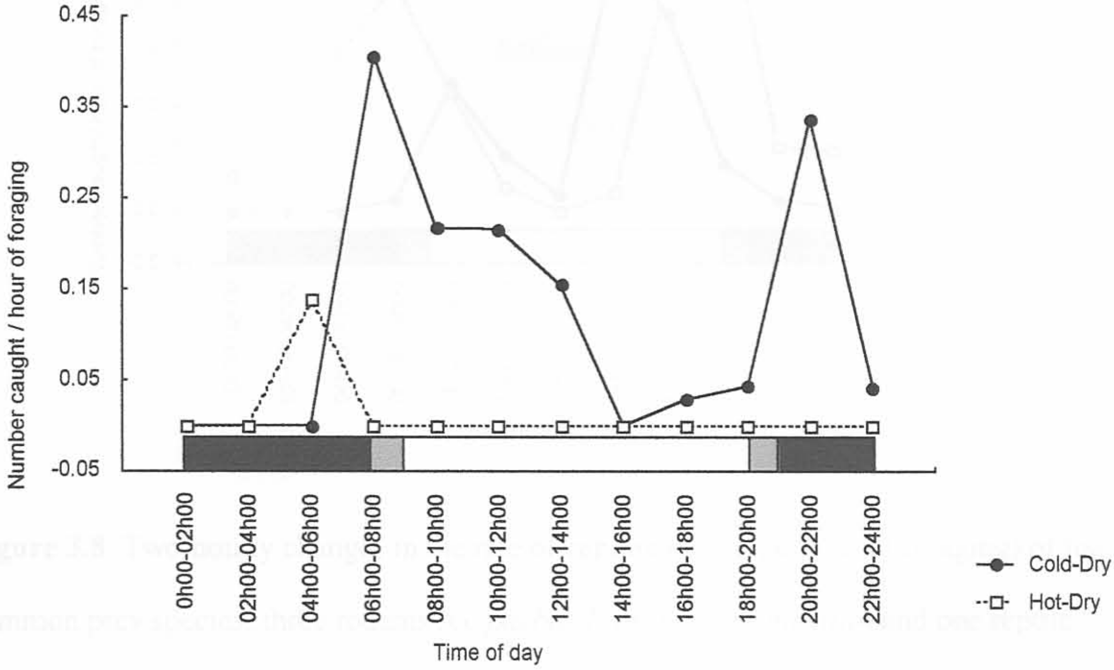
Table 3.6 Comparison of the percentage of the four most common prey categories caught by honey badgers during diurnal and nocturnal foraging. The percentages were calculated from the total number of prey items caught within each prey category during the study period in the KTP.

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

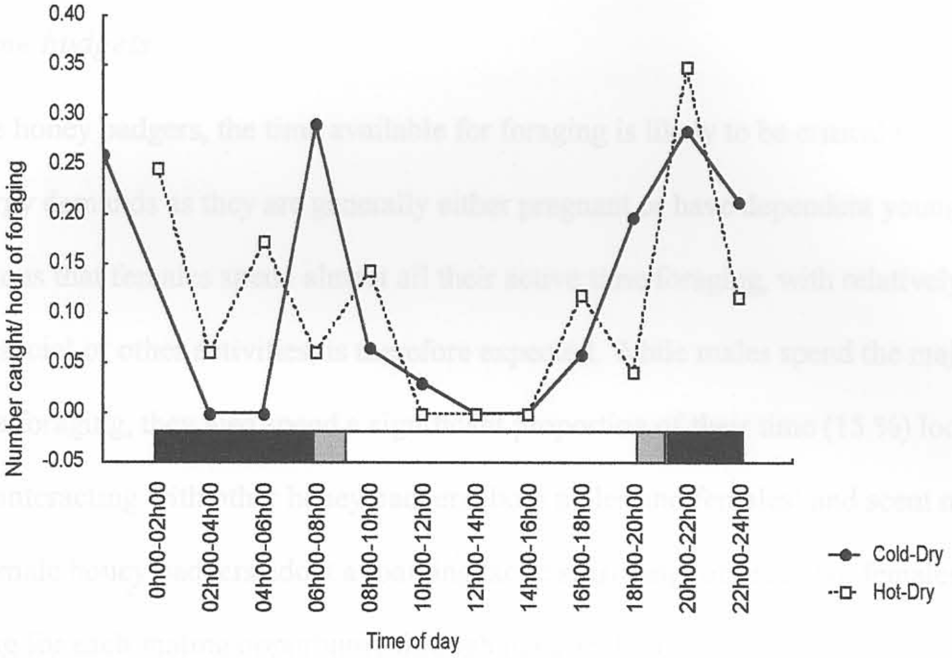
a) Bushveld gerbil *G. paeba*



b) Striped mouse *R. pumilio*



c) Brants gerbil *Tatera brantsii*



d) Barking gecko *Ptenopus garrulous*

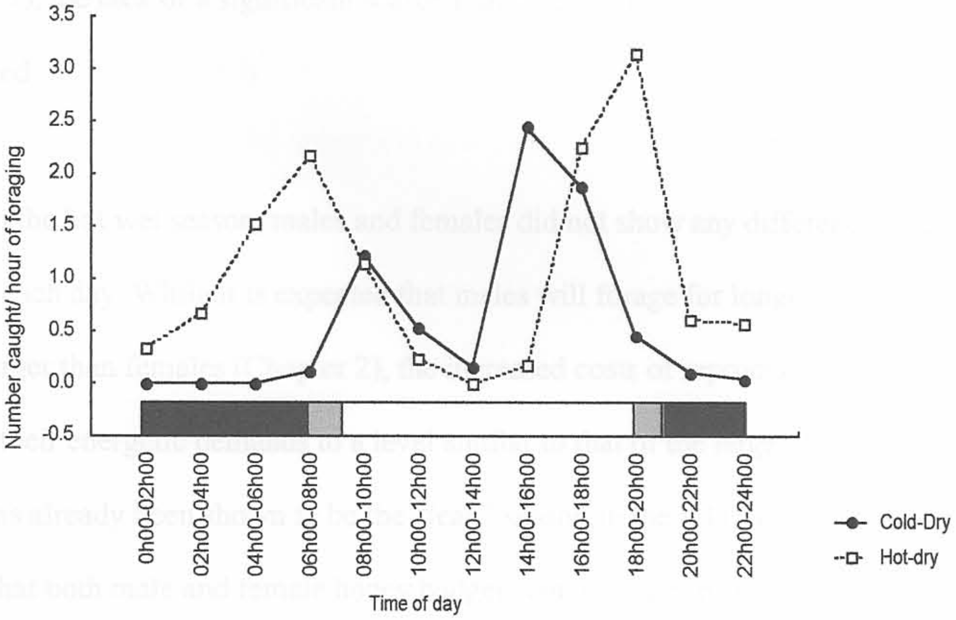


Figure 3.8 Two-hourly changes in the rate of capture (captures/ hour of foraging) of four common prey species; three rodents (*G. paeba, T. brantsii, R. pumilio*) and one reptile (*P. garrulous*) by honey badgers in the KTP.

3.5. Discussion

3.5.1 Time budgets

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

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

3.5.2 Activity schedules

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

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

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

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

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

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

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

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

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

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

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