- Chapter 6 -

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

6.1. Abstract

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

6.2 Introduction

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

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

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

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

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

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

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

6.3 Study area and methods

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

6.3.1. Data collection

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

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

Direct observations (5811 hours) were used to determine the behaviour and frequency of scent marking behaviour, and observation periods ranged from one to twelve days ($\bar{x} = 4$ days, n = 91) with an additional 57 short observation periods (less than 24 hours) ranging from 45 minutes to 20 hours. During all observations honey badgers were observed from the roof of a vehicle 10-30 m away depending on visibility and grass height. All activities were timed and described, and where possible interactions between individuals were filmed (16 mm) and photographed for closer examination. In all cases the GPS position, position of scent mark in the environment, behaviour before and after scent marking, and general description of scent marking behaviour were noted.

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

6.3.2. *Data analysis*

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

6.3.3. Hypotheses related to scent marking in non territorial carnivores

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

6.4. Results

6.4.1. Types of scent marking

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

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

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

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

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

Table 6.1 (continued on next page)

Table 6.1 (cont.)

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

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

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

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

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

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

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

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

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

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

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

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

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

6.4.2. Latrines

6.4.2.1. Latrine descriptions

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

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

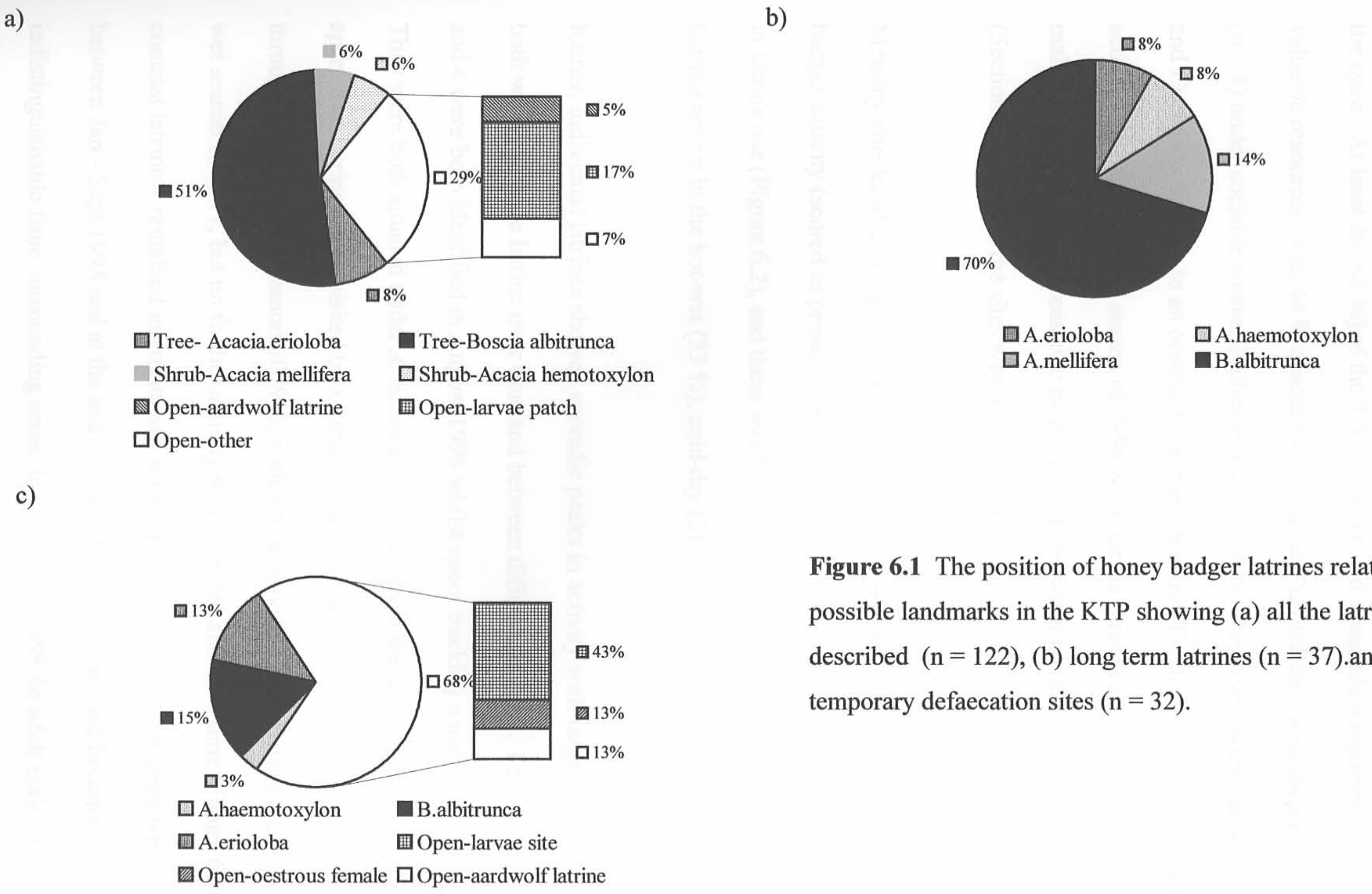

Figure 6.1 The position of honey badger latrines relative to possible landmarks in the KTP showing (a) all the latrines described (n = 122), (b) long term latrines (n = 37).and (c) temporary defaecation sites (n = 32).

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

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

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

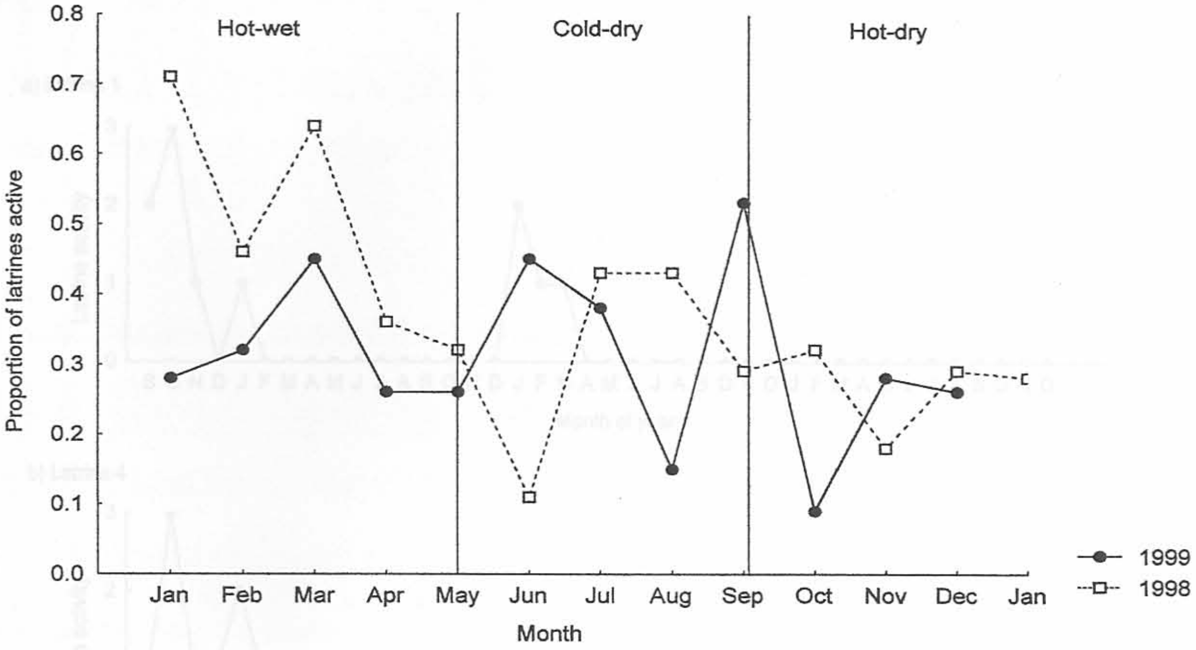

Figure 6.2 Proportion of known honey badger latrines active (scats and/or spoor) during each month of the year for two years in the KTP. Note that there appears to be no seasonal peak in latrine use.

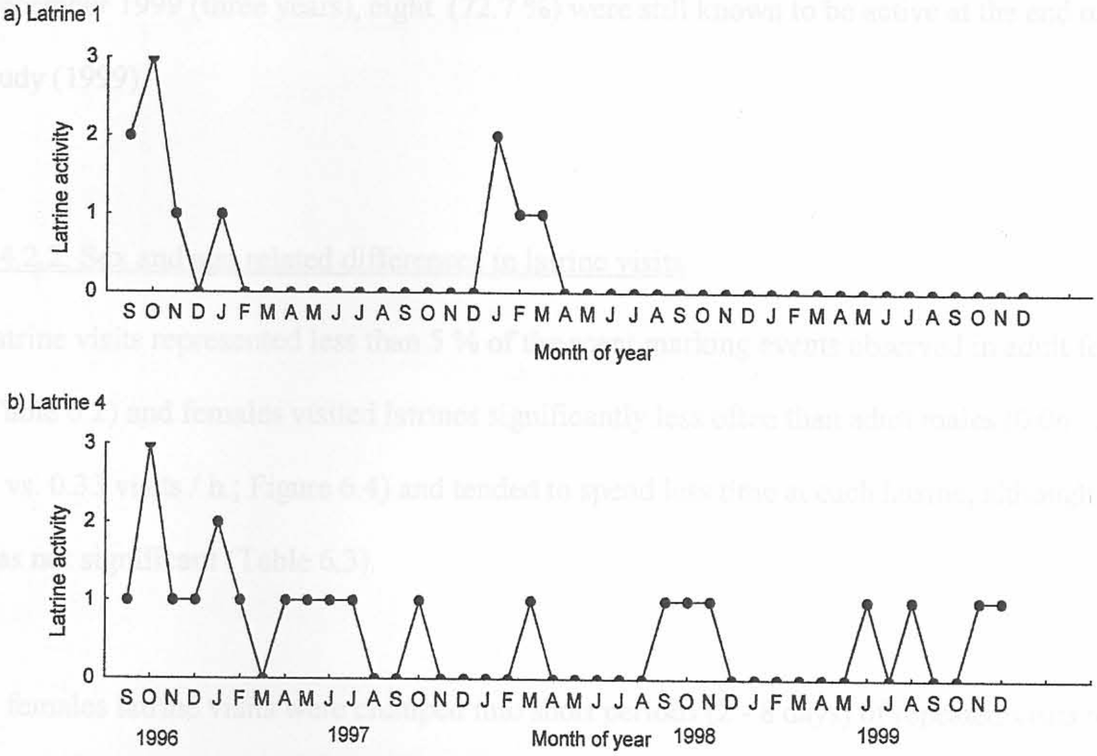

Figure 6.3 Monthly level of activity at two honey badger latrines (1 & 4) for the period September 1996 – December 1999 in the KTP. Note the variation in latrine activity both within and between the two latrines. Activity was scored from 0-3 based on the number of visits in that month where 3 = ≥10 visits,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

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

6.4.2.2. Sex and age related differences in latrine visits

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

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

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

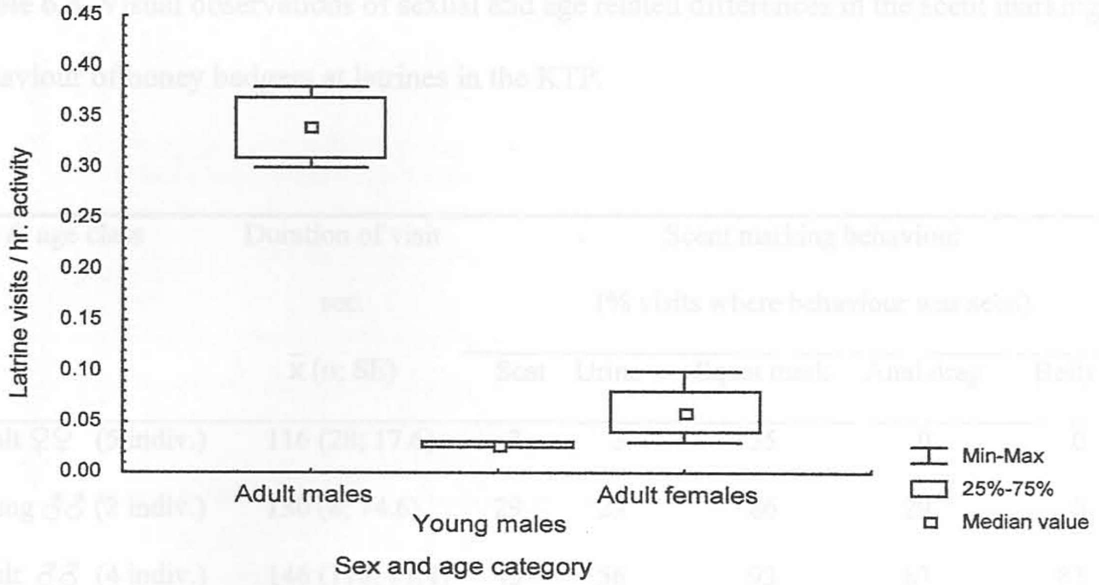

Figure 6.4 The rate of latrine visits in adult female (723 h obs; 5 individuals), adult male (636 h; 4 individuals) and young male (309 h; 2 individuals) honey badgers in the KTP. Kruskal-Wallis test H (2, n = 11) = 8.33; $p < 0.05$ (young males vs. adult males, Q = 2.96, $p < 0.05$; females vs. adult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

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

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

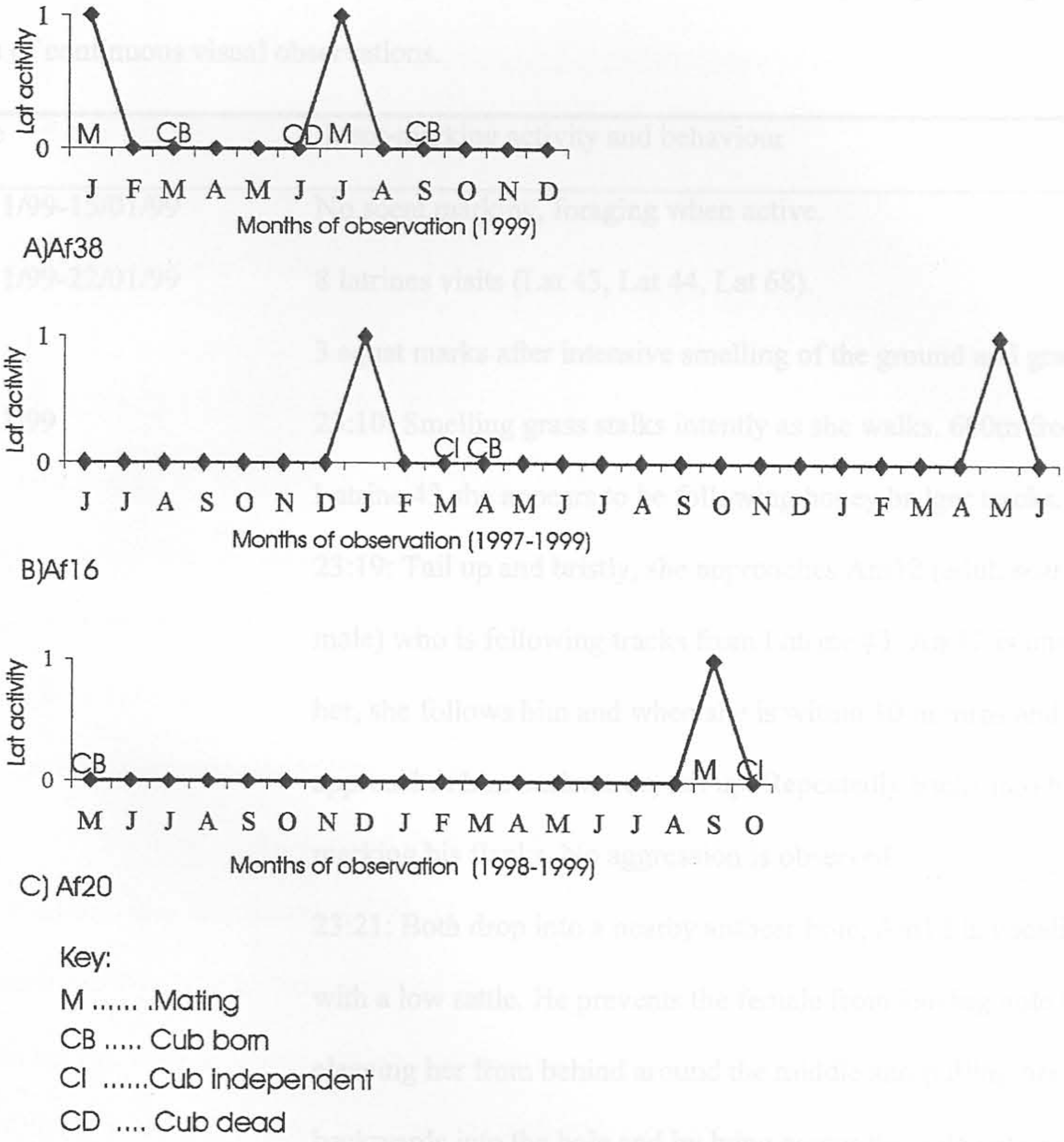

Figure 6.5 The timing of visits to latrines in three habituated female honey badgers over their individual periods of direct observation. Observations of mating, birth of cubs and cub independence are shown to illustrate the association between female latrine visits and reproductive behaviour.

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

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

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

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

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

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

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

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

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

6.4.3. *Token urination*

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

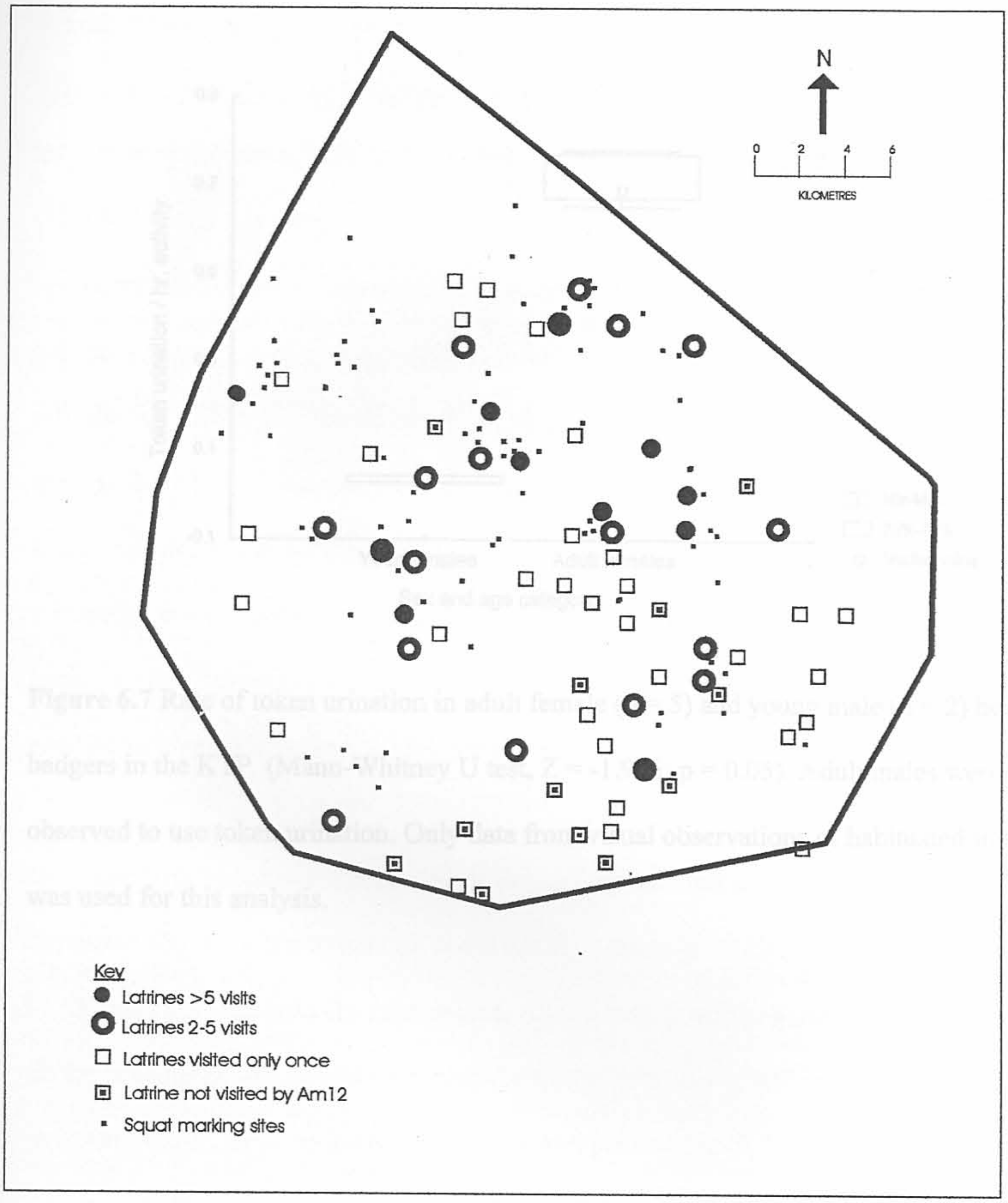

Figure 6.6 Spatial distribution of latrines and scent marking sites within the minimum convex polygon home range outline of an adult male honey badger (Am12). Note the hinterland distribution of latrines and scent marking sites.

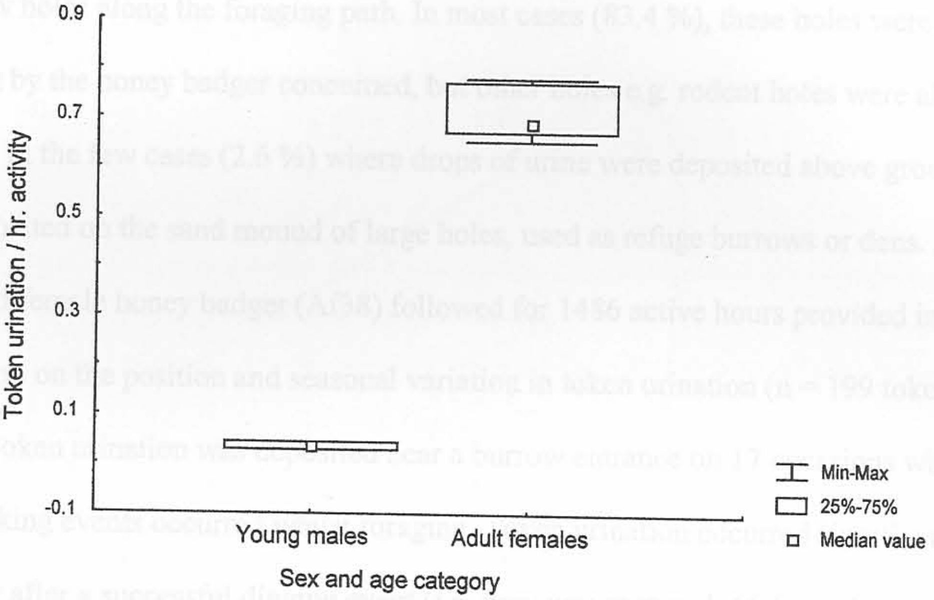

Figure 6.7 Rate of token urination in adult female (n = 5) and young male (n = 2) honey badgers in the KTP (Mann-Whitney U test, Z = -1.936; p = 0.05). Adult males were not observed to use token urination. Only data from visual observations of habituated individuals was used for this analysis.

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

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

6.4.4. Squat marking

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

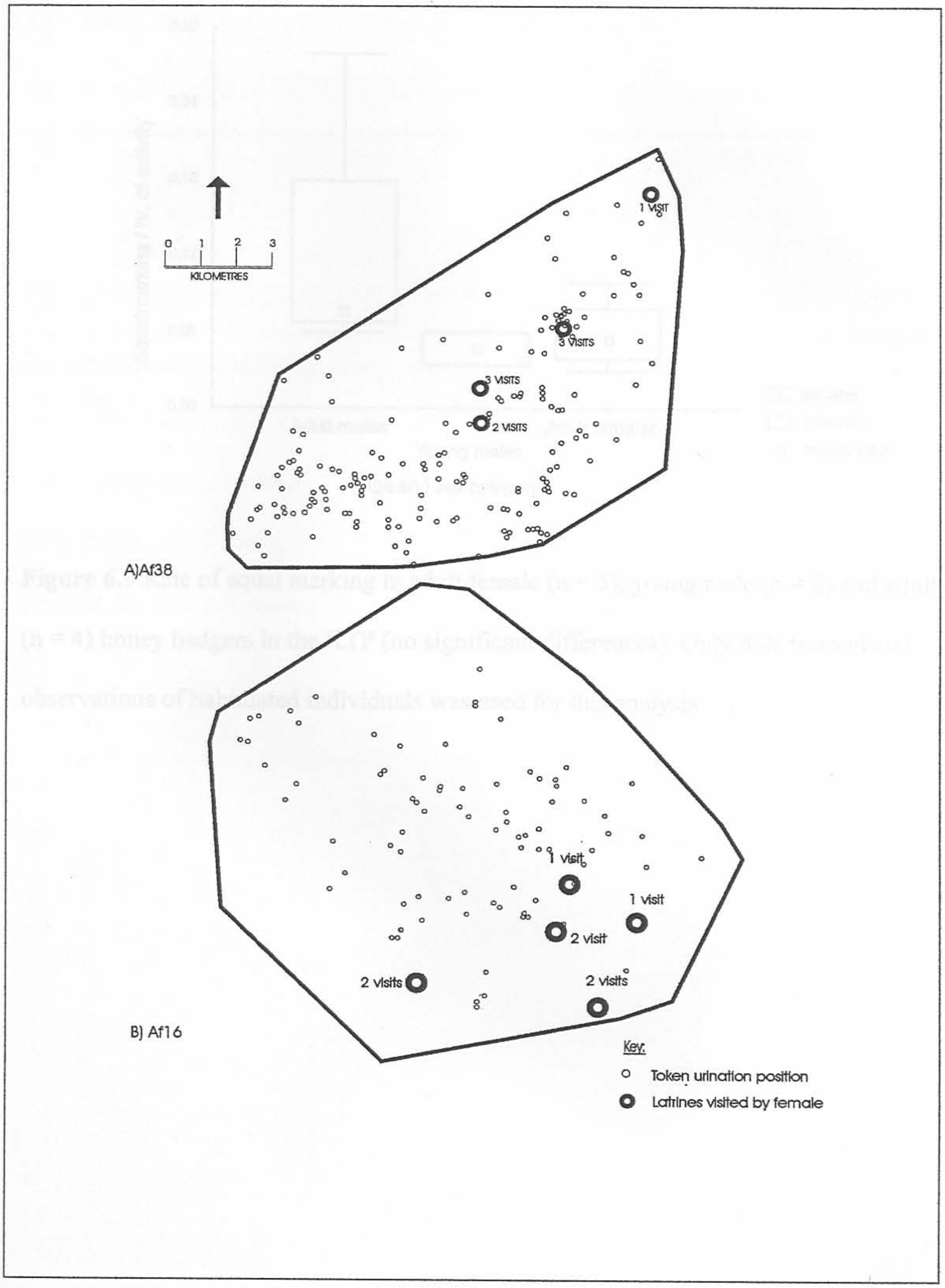

Figure 6.8 Scent marking positions of two adult female honey badgers (Af38, Af16) within their home ranges (105 km^2, 179.7 km^2 respectively). Both the positions of latrines visited by females as well as token urination sites along the foraging paths are indicated.

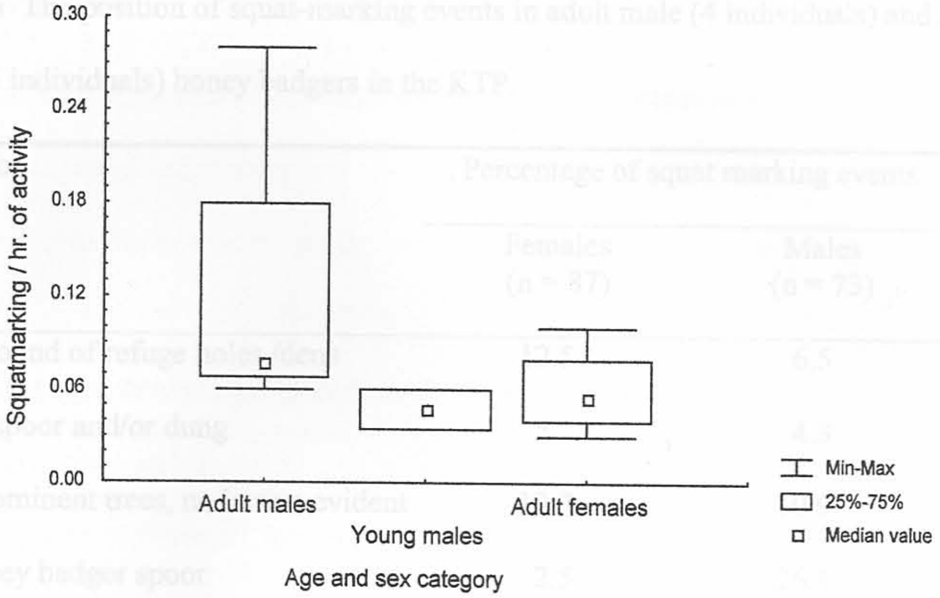

Figure 6.9 Rate of squat marking in adult female (n = 5), young male (n = 2) and adult male (n = 4) honey badgers in the KTP (no significant differences). Only data from visual observations of habituated individuals was used for this analysis.

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

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

6.5 Discussion

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

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

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

6.5.1. Latrines

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

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

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

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

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

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

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

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

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

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

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

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

Recent studies suggest that females often play a more active role in mate choice than previously suspected (Reynolds, 1996). In the honey badger, more than one male was frequently observed around a single female in oestrus, competing (between themselves) for access to the female. The best strategy for a female is to try to mate with the male that is likely to sire successful offspring. It is possible that just as males assess the dominance ranking of other males through marking frequency and scent matching during later interactions, females use latrine visits for a similar function i.e. to assess the dominance status of males in the area and later match the scent found at latrines with males that approach her for mating.

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

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

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

6.5.2. Token urination

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

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

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

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

6.5.3. Squat marking

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

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

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

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

6.6. References

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