



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

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We investigated sexual and seasonal patterns in scent-marking behaviour of the honey badger, by direct observations of habituated individuals (five females, four adult males, two young males). Four categories of scent-marking behaviour were identified: (1) scent marking at latrines; (2) token urination in holes along the foraging path; (3) squat marking at single-use sites; and (4) functional excretion. Females and young males used all four types of scent marking, but adult males were not observed to use token urination. A strategy of hinterland scent marking was used, as was predicted from the large home ranges of both male and female honey badgers. There were significant sexual differences in marking rate: adult males primarily used latrines and adult females favoured token urination. Latrine scent marking in adult male honey badgers provides support for the 'scent-matching' hypothesis. Females visited latrines when they were in oestrus. However, the low level of marking activity during a visit and the intensive smelling suggested a scent-matching function rather than reproductive advertisement. Token urination appeared to be related to the maintenance of spatiotemporal separation in females, although we also observed token urination in young males. While the placement of urine in foraging holes and its relation with successful digging attempts offer some support for the foraging efficiency hypothesis, we consider this unlikely, because we did not observe it in adult males and there was no seasonal pattern. Squat marking occurred under a wide range of conditions in both males and females and may be related to marking valuable resources. It is likely that scent marking in honey badgers has many functions.

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Even solitary animals must have an effective communication system to maintain their social organization 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, underground or in dense vegetation (Clapperton 1989; Alberts 1992; Hutchings & White 2000). As a result, almost all carnivores scent-mark by depositing urine, faeces or other glandular secretions on to features in the environment (Macdonald 1980).

In addition to marking with token amounts of faeces and urine (Macdonald 1985), several mustelid species scent-mark 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, 2002). Mustelids also possess paired anal scent glands, which act as reservoirs for secretions from tubular and sebaceous glands (Gorman & Trowbridge 1989) and the use of anal gland secretions has been described in a variety of mustelid species (Koehler et al. 1980; Erlinge et al. 1982; Clapperton et al. 1988; Dunstone 1993; Lode 1994; 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.

No previous information on the scent-marking behaviour of the honey badger in the wild is available, but 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 is unusual among mustelids in being reversible, as it is in some mongooses and hyaenas. In addition, the

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**Table 1.** Function of scent marking in honey badgers: hypotheses and predictions

Hypothesis	Predictions	Source
(1) Scent matching (males)	Owners mark territory to maximize chance that marks will be detected Owners mark more than subordinates Owners mark themselves with substances used to mark area Owners make themselves available for scent matching Owners remove or replace marks of others. Nonowners should withdraw from owner if scent of owner matches scent marks encountered in the area	Gosling 1982, Gosling & Roberts 2001
(2) Signalling of reproductive status (females)	Sexual differences in scent marking Seasonal changes in female scent-marking rate related to reproductive status Males respond to female marks Females place marks where males are most likely to encounter them	Clapperton 1989
(3) Spatiotemporal separation (females)	Marks placed where neighbouring female is likely to find them No seasonal changes in rates of scent deposition Marking should increase in areas of overlap Individuals must be able to determine freshness of mark	Clapperton 1989
(4) Foraging efficiency (males and females)	No difference between sexes Marking should occur near foraging areas Marking should occur before, during or after foraging bouts Marking should increase when resources are scarce or patchy but replenishing Marks placed where foraging individual is most likely to encounter them	Henry 1977, Kruuk 1995

honey badger has enlarged anal glands in common with members of the genera *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 is particularly interesting because it is a solitary carnivore that does not follow the typical mustelid spacing pattern of intrasexual territoriality (Powell 1979). Our study of honey badgers in the Kalahari (Begg 2001; unpublished data) has revealed that it is a nonseasonal breeder and adult males have large (548 km<sup>2</sup>) home ranges that overlap extensively with other males and encompass the smaller home ranges of young males (187 km<sup>2</sup>) and several females (138 km<sup>2</sup>). There is evidence of a dominance hierarchy between adult males, and groups of two to five individuals sometimes travel together. In contrast, females appear to be loosely territorial: while female home ranges show an average overlap of 25%, they tend to be evenly spaced and adult females avoid each other temporally.

Scent marking is thought to be adaptive and the information conveyed by a mark to contribute to the inclusive fitness of the marker (Gosling 1981). Furthermore, social odours are a limited resource and in many cases require a significant investment of time and energy. Therefore scent marks will be distributed in a way that increases their chance of being discovered by the intended receiver, so that the benefits of producing the scent mark are maximized (an economic marking strategy, Gosling 1981). We investigated the distribution of scent marks in the home ranges of honey badgers. In addition, direct observations of free-living honey badgers allowed us to describe scent-marking events in terms of their temporal and social contexts. We examined the results in relation

to four hypotheses on the function of scent marking in honey badgers (Table 1).

### Hypotheses

(1) The scent-matching hypothesis (Gosling 1982) offers the clearest set of predictions; it was initially developed for territorial animals, but Gosling (1982) suggested that it might be extended to dominance hierarchies. Support for this hypothesis has been documented in species in which males have mutually exclusive territories (Clapperton 1989; Gosling & McKay 1990; Hurst et al. 1996), group territories (Kruuk et al. 1984) and more recently in a spatial system where competing conspecifics have overlapping home ranges (Luque-Larena et al. 2001). Within a dominance hierarchy, this hypothesis suggests that the function of scent marking is to provide an olfactory association between the dominant individual and the predominant scent mark and thus enable a subordinate male to recognize the dominant male in a subsequent encounter. The scent marks therefore provide a way for an individual to avoid the costs of establishing dominance by overt aggression in every encounter (Kappeler 1990; Rich & Hurst 1998). In addition, since scent marks and countermarks provide a continuous record of competitive challenges, Rich & Hurst (1999) suggested that the ultimate function of such competitive signalling may be to provide a reliable advertisement of mate quality to third parties (e.g. females).

(2) The reproductive advertisement hypothesis suggests that scent marks (urine in particular) contain information about the reproductive status and oestrous condition of a female and are used to attract males for mating (Johnston 1983; Gorman & Trowbridge 1989).

(3) Scent marks may also provide a temporal and historical record of an individual's movements and may therefore function as 'railway signals' which mediate spatiotemporal separation of neighbours (Leyhausen & Wolff 1959; Clapperton 1989). Given the regular spacing of female home ranges and lack of interaction between female honey badgers, we predicted that their spatiotemporal separation is maintained through scent marking.

(4) The foraging efficiency hypothesis relates scent marking to resource dispersion and 'book keeping' (Henry 1977). It suggests that marking behaviour is used by an individual to signal to others where it is feeding and thereby enables individuals to partition resource use and increase foraging efficiency (Kruuk 1995).

## METHODS

### Study Site

We carried out the study from July 1996 to December 1999 (42 months) in the Kgalagadi Transfrontier Park (KTP), which encompasses an area of 36 200 km<sup>2</sup> and consists of the Kalahari Gemsbok National Park, South Africa (KGNP) and neighbouring Gemsbok National Park, Botswana. It is a semidesert region; Acocks (1988) described the vegetation as the western form of Kalahari thornveld with an open savannah of *Acacia haemotoxylon* and *Acacia erioloba* with desert grasses.

### Study Animals

A permit for the capture of live honey badgers was obtained from South African National Parks and all immobilization and sedation was done by K. Begg, who holds a licence for the Chemical and Physical Restraint of Wild Animals (Veterinary course, Harare 1995). Fresh honey badger tracks were followed on foot by a Khomani-San tracker (K. Kruiper) and one researcher until the honey badger(s) was in sight. It was approached downwind to within 10–50 m, chased and caught in robust hand nets. Captured individuals ( $N=67$ ) were wound up inside the net to minimize their movement and immediately hand injected in the rump with an immobilizing sedative drug, Zoletil (tiletamine hydrochloride with the benzodiazepine derivative Zolazepam in 1:1 combination; mean dosage 5.2 mg/kg). No honey badgers were injured as a result of this method of capture and this technique was considered highly efficient, with a minimal amount of stress and little potential for harm compared with other methods such as darting and cage trapping. On one occasion an adult female rolled into the sun during recovery and died as a result of heat stress (ambient temperature 36°C). Subsequent to this fatality, recovering individuals were placed in a hole in the shade (up to 50 cm deep) with a few branches covering the entrance and watched from afar. No further problems were observed. Honey badgers typically recovered after 50–180 min (mean 71 min;  $N=18$ ).

Whilst sedated, 25 individuals (13 females and 12 males) were fitted with Telonics (Mesa, Arizona, U.S.A.) MOD 400 (180 g for adult males weighing 10–12 kg) or MOD 335 radiocollars (105 g for adult females and young males weighing 5.7–7 kg). All collars were removed from honey badgers before the end of the battery life or at the end of the study period. A wildlife veterinarian implanted 10 of the radiomarked adults (five females and five males) and three large cubs (one male, two females) with intraperitoneal radio implants (Telonics IMP/400L; 31 × 94 mm). Each implant was inserted through a 45-mm incision into the peritoneal cavity and was 'free floating', allowing the implant to stabilize on its own. Two layers of single interrupted sutures closed the wound. Animals were injected with penicillin before release. Three of the adult females were known to conceive and give birth after implantation. Implants lasted the full duration (20–22 months) and it was decided that they should not be removed since this would increase the chances of postsurgical infection and implants were frequently encapsulated within the abdomen wall (D. Grobler, personal communication). Since honey badgers appear to be short lived (3–8 years) in the Kalahari, implants were considered to be of minimal threat to the individual. An implant recovered from a female honey badger killed by a leopard 13 months after implantation showed no sign of wear. There was no evidence that any animal died or was injured as a direct result of either radiocollars or radio implants.

We weighed and measured (body length, shoulder height, neck circumference, testes) all captured animals and recorded physical features of each animal (e.g. ectoparasites, scars and wounds). Adult males were broadly divided into two age categories based on tooth wear, body size and condition: young adult (estimated age 1–3 years) and adult (older than 3 years). In adults tooth wear was most noticeable on the third incisor on the upper jaw, which in young adults is noticeably different to other incisors and resembles a canine, but is quickly worn down to resemble the other incisors in older badgers. On capture, males could also be clearly separated into these two groups on the basis of testes size (calculated as testes area: length × breadth) and body mass, although they showed no differences in body length or shoulder height (unpublished data). We further divided older adult males into males with and those without a back scar, on the assumption that 'scarback' males were older than nonscarback males, as there is some evidence that the scar develops over time. 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 (Begg 2001; unpublished data). Since young females dispersed more than 50 km from the natal home range on independence (estimated age at independence is 12–16 months,  $N=7$ ; unpublished data), we could not assess young female scent-marking behaviour. Nine radiomarked adult badgers (five females with cubs and four males) and two young males were habituated to the vehicle until they could be followed without any obvious influence on their behaviour.

**Table 2.** Study population used for analysis of scent-marking behaviour in the honey badger

Individual	Total hours observed	Active hours observed	Months followed
<b>Adult females</b>			
Af38	1486	305	12
Af20	189	69	20
Af25	172	61	17
Af16	771	201	17
Af07	263	87	17
Total	2881	723	83
<b>Adult males</b>			
Am43	303	98	7
Am12	1226	379	24
Am24	202	79	8
Am42	304	80	10
Total	2035	636	49
<b>Young males</b>			
Ym36	123	109	4
Ym42	422	200	8
Total	545	309	12
<b>Total</b>	<b>5461</b>	<b>1668</b>	

## Data Collection

We directly observed habituated individuals (5461 h excluding search time) to obtain information on scent-marking behaviour. The total time spent with each individual ranged from 123 to 1486 h (Table 2). Observation time was further divided into observations of active behaviour (active time; 1668 h) and resting behaviour (Table 2). An individual was considered to be resting when it was out of sight in a burrow for more than 30 min with no sound of movement, digging or vocalizations or lying curled up on its side above ground with its eyes closed. We followed habituated individuals for continuous periods of 1–12 days (two observers, mean 4 days,  $N=91$  observation periods) with an additional 57 short observation periods (less than 24 h) of 45 min to 20 h, where an observation period was considered to have ended if contact with an individual was lost for more than 30 min. During active time, individuals were followed in a vehicle 10–30 m away depending on visibility and grass height, with one observer on the roof. During resting time, the vehicle was parked within 10–30 m of the resting individual and one observer checked on the position and activity of the resting individual every 15–30 min through visual or radio contact. All activities were timed and the GPS position, specific position of the scent mark in the environment, behaviour before and after scent marking, and general description of scent-marking behaviour were recorded into a Dictaphone and later transcribed on to data sheets.

Latrines (common defecation sites containing signs of at least two independent visits by a honey badger) could be located only by following (visual or tracking) honey badgers and were thus always active on first identification. They were assigned individual consecutive numbers and we noted their GPS position, size, shape, habitat

and prominent landmarks. We visited a sample of latrines (11 in 1997, 24 in 1998, 46 in 1999 as more latrines were located) at the beginning of each month to assess changes in use over time and noted all signs of activity (tracks, scats, urine). For each latrine we estimated relative frequency of use by counting the number of new scats deposited during a single month. To assess temporal patterns in latrine use, we classed each latrine as either active, that is evidence (tracks, scat, urine) of at least one visit by a honey badger, or inactive, that is, no evidence of any visits at each monthly check. The proportion of overall latrines checked that were active was then calculated for each month for 3 years. At each visit, we removed all scats for dietary analysis but walking on the latrine was kept to a minimum. To assess the affect of removing scats from the latrines, we treated 10 long-term latrines as controls and at these latrines, new scats were counted and broken up (to prevent recounting) but were not removed. There was no significant difference (Mann–Whitney  $U$  test:  $U=100$ ,  $N_1=23$ ,  $N_2=10$ , NS) in the average number of visits per month between long-term (see Results) latrines where scats were removed and latrines where scats were not removed.

The positions of scent-marking sites were plotted (GPS coordinates imported into ranges V; Kenward 1991) for two adult females (Af38, Af16) and one adult male (Am12), which had all been intensively followed for more than 1 year and observed for more than 700 h. Hinterland and perimeter marking were compared, with a technique adapted from studies of hyaena territoriality (Gorman & Mills 1984; Richardson 1991), where a matrix is superimposed over the entire home range (100% minimum convex polygon; male= $4 \times 4$ -km grid overlay; female= $1 \times 1$ -km grid overlay). A grid square was categorized as a perimeter square if it touched the home range boundary line. If less than half of this perimeter square was inside the home range area then the next square in was also denoted a perimeter square. As a result, the perimeter zone was at least 2 km wide for the adult male and at least 0.5 km wide for females. We used chi-square analysis to compare observed and expected frequencies of hinterland (core area) and perimeter marking with expected frequencies calculated from the relative area of the border and hinterland parts of a range.

The patterns of scent marks within a home range were visualized by the nearest-neighbour mapping technique (Gosling 1981; Roberts & Lowen 1997). The result of this mapping technique is an irregular polygon with a gap at one point, which is subjectively closed. The position and size of the polygon within the home range were used to provide information on marking economics. We used the program Sadie to investigate whether scent marks were significantly random, regular or aggregated by using counts of scent-marking events per grid cell (Perry et al. 2002).

In all cases, the individual was the basic sampling unit for the statistical tests. Quantitative data on the rates of scent marking were calculated as scent-marking events per active h per individual, and compared in different age/sex groups using nonparametric Kruskal–Wallis tests (latrine scent marking, squat marking) with post hoc

**Table 3.** Description of scent-marking behaviours identified in honey badgers

Category	Description	Type and position
<b>(1) Primary</b>		
Anal drag	Individual assumes squatting position with pelvis depressed so that anus touches ground. Tail raised in arc over body. Anus dragged along substrate in straight line (<0.5 m) or circle	Anal gland secretion, above ground, frequently at latrine
Squat mark	Similar to anal drag. Individual squats and presses anus to ground repeatedly (1–52 times consecutively). Frequently occurs after intensive smelling with nose touching ground	Anal gland secretion, above ground, at latrines and single-use sites
Token urination	Small amounts (few drops) of urine dribbled from squatting position, considered primarily communicative rather than eliminatory in function	Urine, in holes along the foraging path
Defecation	Defecation from squatting position both in association with other primary scent-marking behaviour at latrines and as independent defecation events	Faeces, above ground (i.e. latrines) or in hole when deposited independently
Squat urination	Large amounts of urine deposited in single event. Likely to be used for both elimination and defecation	Urine, above ground, in males frequently at latrines
<b>(2) Secondary</b>		
Body–neck rubbing	Dorsal surface of belly, neck and chin rubbed on substrate, with front legs splayed and tail raised above body. Occurs after primary scent marking and usually leads to vigorous scratching	On primary scent-marking site, may release scent from glands in neck region but self-anointment likely
Scratching and rolling	Intensive periods of scratching and rolling observed during and after intensive scent-marking event	On primary scent-marking site, may release odours but self-anointment likely

nonparametric multiple comparison testing (*Q* test; Zar 1999) and Mann–Whitney *U*-tests (token urination). For analysis of seasonal changes in scent-marking rate we distinguished three seasons: the hot–wet season 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 from May to August when the mean monthly temperature is below 20°C and rainfall is rare; and the hot–dry season 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).

## RESULTS

### Types of Scent Marking

Overall, five primary (anal drag, squat marking, token urination, defecation and urination) and two secondary (body–neck rubbing, and scratching and rolling) types of scent-marking behaviour were identified (Table 3). 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. The release of the evacuate was associated with defensive behaviour that included a loud ‘rattling’ vocalization, an erect tail, standing tall, charging and piloerection, and it was considered part of a threat display. Since the main function of this behaviour appears

to be defensive rather than intraspecific information transfer, we do not discuss it further here.

We directly observed 1034 scent-marking events categorized into four groups: scent marking at communal areas or latrines involving a combination of scent-marking behaviours (22.8%, *N*=236), token urination in holes (51.3%, *N*=530), squat marking/anal drag at single-use sites (15.4%, *N*=160) and functional excretion including both independent defecation and urination events (10.5%, *N*=108). It is likely that some functional excretion events were missed when badgers excreted in the resting burrows or immediately on leaving a resting burrow. While scats and urine (unaccompanied by other scent-marking behaviour) are likely to have some marking function, insufficient data precludes further analysis.

### Sexual and Age Differences

While both sexes were observed to squat mark and use latrines, adult males did not token urinate (Table 4) and adult females did not anal drag or belly–neck rub at latrines or single-use sites (Table 5). The two young males used all scent-marking types, except for the belly–neck rub. The absence of the belly–neck rub in young males and females suggests that it has a specific function such as self anointment with the scent, and is not simply a form of grooming.

In both young males and adult females, token urination was the most common type of scent marking; latrine visits were the least common and squat marking was intermediate (Fig. 1). However, token urination was

**Table 4.** Overall number and type of scent-marking events recorded in male and female honey badgers

Age and sex	Type of scent-marking behaviour		
	Latrines*	Squat mark	Token urination
Adult females (N=5)	31 (5.1)	87 (14.4)	486 (80.5)
Adult males (N=5)	190 (78.8)	51 (21.2)	0
Young males (N=2)	15 (18.5)	22 (27.2)	44 (54.3)

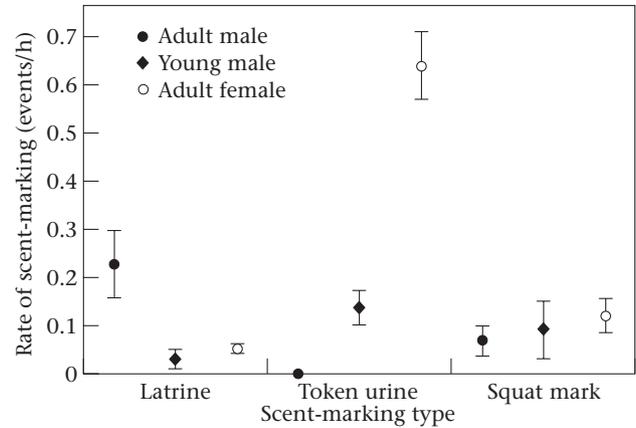
Percentages are shown in parentheses.

\*Number of latrine visits.

significantly more frequent in adult females ( $\bar{X} \pm SE = 0.64 \pm 0.07$  urine marks/h) than young males ( $0.14 \pm 0.04$  urine marks/h; Mann–Whitney test:  $U = 10$ ,  $N_{\text{female}} = 5$ ;  $N_{\text{young male}} = 2$ ,  $P < 0.05$ ; Fig. 1). There were no significant differences in the rate of squat marking between age and sex classes (Kruskal–Wallis test:  $H_2 = 0.86$ ,  $N = 11$ , NS; Fig. 1).

The mean rate of latrine scent marking was significantly higher (Kruskal–Wallis test:  $H_2 = 7.43$ ,  $N = 11$ ,  $P < 0.05$ ; young males versus adult males:  $Q = 2.96$ ,  $P < 0.05$ ; females versus adult males:  $Q = 2.43$ ,  $P < 0.05$ ; females versus young males;  $Q = 0.63$ , NS; Zar 1999) in adult males ( $\bar{X} \pm SE = 0.23 \pm 0.07$  visits/h,  $N = 4$ ) than in either females ( $0.05 \pm 0.009$  visits/h,  $N = 5$ ) or young males ( $0.03 \pm 0.02$  visits/h;  $N = 2$ ; Fig. 1). In addition, 79% of all scent-marking events by adult males occurred at latrines, compared to only 19% by young males and 5% by adult females (Table 4). The sample sizes were too small to test for significant differences in the frequency of latrine scent marking within adult males of different rank, that is, scarbacks (dominant) versus nonscarbacks (subordinate), but there was a trend for scarbacks to scent-mark at latrines more frequently ( $\bar{X} \pm SE = 0.35 \pm 0.05$  visits/active h,  $N = 2$ ) than nonscarbacks ( $0.10 \pm 0.02$  visits/active h,  $N = 2$ ).

There were no significant individual differences in the duration of latrine visits (ANOVA:  $F_{11,128} = 4.37$ ,  $P < 0.015$ ), but there were marked sexual and age-related differences

**Figure 1.** The mean  $\pm$  SE rate of scent marking observed in adult male (636 h;  $N = 4$ ), young male (309 h;  $N = 2$ ) and adult female (723 h;  $N = 5$ ) honey badgers.

in latrine marking behaviour (Table 5). Scent marking occurred on only 55% of female latrine visits and generally consisted of one to four squat marks in the bare area of the latrine, with a scat and urine left on only three occasions (Table 5). Intensive smelling and a slow walk across the entire latrine with the tail erect characterized all female latrine visits.

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. During scent marking, the bare sand, as well as logs, tree roots and grass tufts within the latrine area, was marked, the penis was erect and urine was frequently dribbled during the squat mark and anal drag. In addition, adult males deposited scats on latrines on 43% of their latrine visits and these provided long-term signs of latrine use (Table 5). In adult males, in particular, latrine visits varied in duration from brief visits ( $< 1$  min) with limited scent marking (squat marking and/or defecation) and cursory smelling to intensive, longer visits (maximum 10 min) where the male repeatedly scent-marked over the entire latrine area using the full repertoire of scent-marking behaviours described. The latrine scent-marking behaviour of young males was markedly simpler and less

**Table 5.** Observations of sexual and age-related differences in the scent-marking behaviour of honey badgers at latrines

Sex and age class	Duration of visit (s)	No. of latrine visits	Scent-marking behaviour*					
			None	Scat	Urine	Squat mark	Anal drag	Belly rub
Adult female (N=5)	127 $\pm$ 16.7	31	45	3	3	55	0	0
Young male (N=2)	261 $\pm$ 41.4	15	0	29	29	86	29	0
Adult male (N=4)	164 $\pm$ 50.5	190	0	43	56	93	83	83

Means are shown  $\pm$  SE.

\*Percentage of overall visits where behaviour was seen.

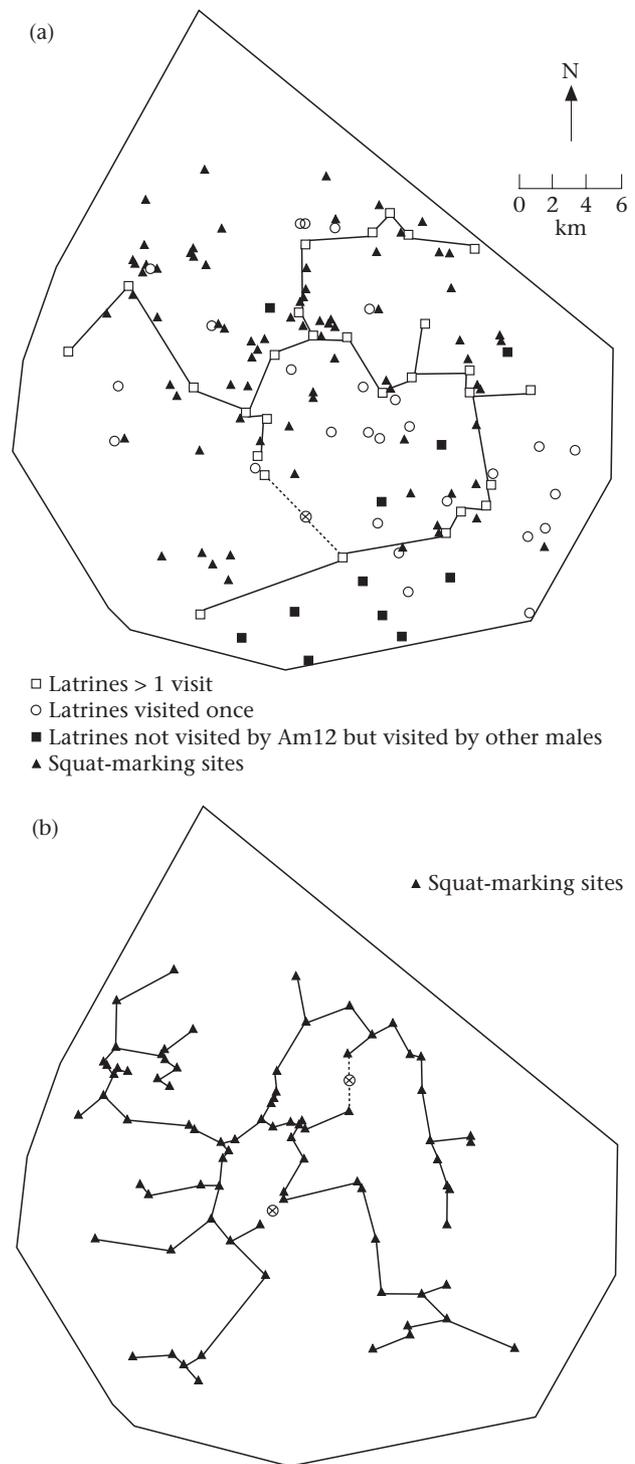
intense than in adult males (Table 5): it consisted primarily of squat marking (86%) with occasional anal drags, urination and defecation.

### Spatial Pattern of Scent Marks

Figures 2 and 3 show the patterns of scent-marking sites (permanent latrines, squat marking positions and token urination) within the home ranges of two habituated individuals. In both cases, nearest-neighbour mapping shows inner polygons of scent-marking sites with a number of branches extending towards the boundary. The pattern is clearest in the mapping of latrines used more than once by the adult male and least clear in the mapping of male squat-marking sites. In all cases significantly fewer scent marks were found in the perimeter area of the home range than in the core (Table 6). Analysis by Sadie of one male, two females showed that latrines and token urination sites were no more aggregated than expected from a random permutation of counts. However, the squat-marking sites of the adult male were significantly more aggregated than expected (index of aggregation = 1.31,  $P < 0.05$ ).

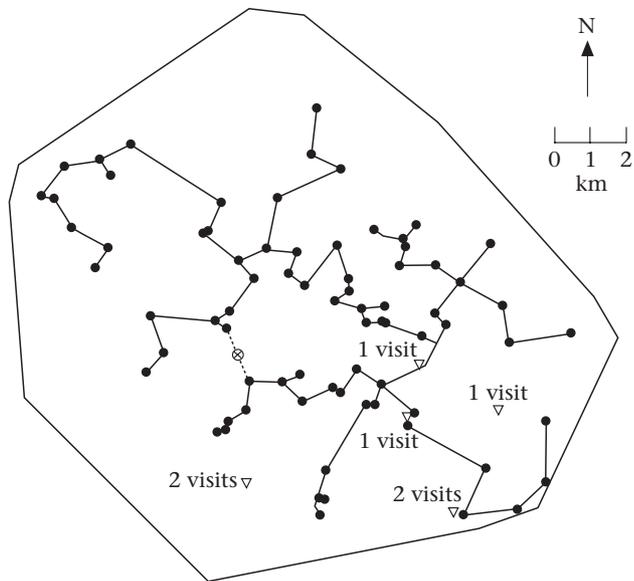
We identified 122 latrines during the study. They consisted of a patch of ground laid bare by frequent scent marking and scratching activity with 2–52 scats deposited above ground on the bare area. They varied in size (2–20 m<sup>2</sup>; mean 6 m<sup>2</sup>) and shape from long paths of activity (0.5 × 12 m) to circular latrine patches. The largest latrine consisted of four circular latrine patches joined by 11 paths amongst *Acacia 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 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.

Latrines were most commonly found on dune slopes (70.2%), followed by dune troughs (23.8%), but seldom on dune crests (6.4%). In 15 cases, latrines were found under the same *Boscia albitrunca* trees as hyaena latrines. 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 and position. Long-term latrines were active for more than a single season (54%,  $N = 37$ ) while 'temporary defecation sites' (TDS, as in Roper et al. 1996) were active for less than a single season and often for only a few days (46%,  $N = 32$ ). Long-term latrines and TDS showed significant differences in position (chi-square test:  $\chi^2_2 = 41.05$ ,  $P < 0.01$ ). The majority of long-term latrines were beside or under trees (78%), which are prominent visual landmarks in the open Kalahari landscape (at least from a human perspective), with the remainder beside *A. mellifera* and *A. haemotoxylon* shrubs (22%). In addition to being visual signposts, trees were frequently visited by honey badgers during foraging activities both to look for potential food items (e.g. skins, rodents and nesting birds) and for the shade they provided for sand bathing and resting. Shade also retards desiccation and this may prolong the odour value of scent marks. No long-term latrines were found in the open.



**Figure 2.** Spatial distribution of (a) latrines and (b) squat-marking sites within the minimum convex polygon home range outline of an adult male honey badger, Am12 (822 km<sup>2</sup>), with nearest-neighbour mapping. The dotted line represents the line subjectively drawn after the mapping process is complete to close the polygon. Since the drawing of this final line is a subjective process, where necessary two possible lines are shown.

In contrast, the majority of TDS were in the open (68%,  $N = 22$ ) with the remainder under trees (13%) or bushes (19%). At least 20 (63%) of the TDS were located



- Token urination positions
- ▽ Latrines visited by female

**Figure 3.** Spatial distribution of token urination sites and latrines within the home range of an adult female, Af16 (201 km<sup>2</sup>), showing the results of nearest-neighbour mapping of the token urination sites. The dotted line represents the line subjectively drawn after the mapping process is complete to close the polygon.

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 oestrous female in a burrow.

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, such as 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. Detailed observations of token urination in female Af38 ( $N=199$  token urination events) showed that drops of urine were deposited near a burrow entrance on 17 occasions, while 182 scent-marking events occurred in

**Table 7.** The position of squat-marking events in adult male ( $N=4$ ) and adult female ( $N=5$ ) honey badgers

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

foraging holes when the honey badger was foraging. Independent squat-marking events occurred above ground but under a wide variety of circumstances (Table 7). In all cases squat marking was accompanied by a 'bottlebrush' tail and intensive smelling and nose dabbing of grass stalks or sand.

## Temporal and Social Contexts

### Latrines

Monthly checks of 11 latrines in 1997, 24 latrines in 1998 and 46 latrines in 1999, showed no clear seasonal pattern in latrine use with 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. 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; both were under *A. haemotoxylon* shrubs in the same habitat and were 2.3 km apart. The latrines were visited by a variety of honey badgers 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. In contrast, latrine 4 remained intermittently active throughout 1997, but there were few visits between January and September 1998 and at

**Table 6.** Chi-square tests of the density of scent marks in the home range core (C) and periphery (P)

Individual	Area (km <sup>2</sup> )		Proportion of total area		Density of scent marks (marks/km <sup>2</sup> )		$\chi^2$
	C	P	C	P	C	P	
Male Am12, Latrines	496	352	0.58	0.42	0.09	0.02	18.78*
Male Am12, Squat marks	496	352	0.58	0.42	0.12	0.06	9.57*
Female Af38, Token urine	65	42	0.57	0.43	2.10	1.20	14.24*
Female Af16, Token urine	119	82	0.59	0.41	0.66	0.11	34.36*

For males data are presented for the density of latrines sites and squat-marking sites; for females only the density of token urination sites is presented.

\* $P < 0.01$ .

the end of this period the latrine had become visually indistinguishable from surrounding areas. In September 1998 an adult male visited the latrine, and it continued to be active until the end of 1999 (end of the study). Of the 11 latrines identified in the hot-dry season of 1996 and checked each month until December 1999 (3 years), eight (72.7%) were still active at the end of the study (1999).

We regularly observed (1226 h) a habituated scarback male (Am12) over a 2-year period. Of the 66 latrines identified within his home range, 11 were not seen to be visited by him although they were known to be active during the period of study, and at least 31 (47%) were also used by other males (Fig 2a). On average four latrines (range 0–10) were visited each day, with 47% of the latrines visited more than once and 10 on more than five occasions. Am12 showed no significant seasonal differences in the mean rate of latrine visits per active h (cold-dry:  $0.31 \pm 0.05$  visits/h; hot-dry:  $0.42 \pm 0.11$  visits/h; hot-wet:  $0.45 \pm 0.19$  visits/h; Kruskal–Wallis test:  $H_2=2$ ,  $N=33$ , NS; where the sampling unit was a continuous 24-h observation period).

In females, latrine visits were clumped into short periods (2–8 days) of repeated visits to two to five latrines separated by up to 14 months of no latrine visits. 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. Eight females were observed to visit latrines on 31 occasions (five habituated females and three spot observations), and on three occasions, two different females visited the same latrine but at separate times.

The timing of these visits suggests that they were used by females to find or assess males for mating. On seven occasions female latrine visits culminated in sexual interactions (courtship and mating), on two occasions they coincided with the dispersal of a full-grown cub and on five occasions a new cub was born within 2 months of known latrine visits. On six latrine visits (3%) adult males also showed flehmen where their lips were pulled back in a grimace and the ground or grass was licked. By directly following scent and tracks from latrines, adult males encountered females on three occasions and other adult males on nine occasions.

On 20% of latrine visits, adult males vocalized while scent marking, using a low rattle/grunt also heard during male–male interactions. On 11 occasions, groups of two to five males (Begg 2001) 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. Observations suggest that the dominance hierarchy of adult males affects the position of scent-marking events on the latrine. On all occasions when a scarback adult male was observed at a latrine with a nonscarback adult male ( $N=4$ ), the scarback prevented the nonscarback and other young males from marking near the centre of the latrine by physical ‘pushing’ and intimidation.

#### Token urination and squat marking

Seasonal differences in the rate of token urination in females were not significant (Kruskal–Wallis test:

$H_2=1.18$ ,  $N=10$ , NS), although urine was deposited slightly more frequently in the hot-dry season ( $0.77 \pm 0.12/\text{km}$ ,  $N=3$  females) than in the hot-wet season ( $0.53 \pm 0.19/\text{km}$ ,  $N=3$ ) with the cold-dry season intermediate ( $0.63 \pm 0.17/\text{km}$ ,  $N=4$  females). There was little difference in the rate of token urination in Af38 during different reproductive states, that is, in oestrus ( $0.62/\text{km}$ ), pregnant ( $0.58/\text{km}$ ) and cub rearing ( $0.72/\text{km}$ ). 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:  $L_1=0.426$ ,  $L_2=0.579$ ,  $P<0.05$ ), but only 34% of successful digging events ( $N=359$ ) were scent marked. Insufficient data were available for a similar analysis in young males.

In adult males flehmen was observed on 13 occasions (25%) in association with single squat-marking events (i.e. not at latrines), and on six of these events fresh tracks of other honey badgers were seen at the scent-marking site. No seasonal patterns in squat marking were observed.

## DISCUSSION

In common with other mustelids, scent marking is an important form of communication in the honey badger, which regularly marks objects within its environment. Considering the 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) and sexual differences in marking behaviour, it is likely that a variety of messages are sent, particularly at latrines where a combination of scent-marking odours are used. In the European badger, *Meles meles*, Stewart et al. (2002) found significant differences in where badgers placed faeces and subcaudal gland marks on latrine surfaces and suggested several possible functions for latrine visits. A similar situation is likely to be true of honey badgers.

While the latrines and token urination marks appeared to be randomly distributed throughout the home range, we observed a hinterland marking strategy (Gorman & Mills 1984), with a clustering of marks towards the centre of the home range at some distance from the home range boundary. This was expected given large home ranges and has been well documented in other carnivore species including the brown hyaena, *Hyaena brunnea* (Gorman & Mills 1984; Mills 1990). In addition, marks are placed in specific positions, such as under trees at the latrine site or in a foraging hole for token urination. The positioning of long-term latrines under visual landmarks such as trees, drops of urine in foraging holes and squat marks and temporary defecation sites at valuable resources all support the hypothesis that honey badgers make strategic decisions about where best to place the marks to maximize the chance that they reach their intended recipients (Gosling 1981; Alberts 1992; Roberts 1997). Given the large home ranges of honey badgers the overall patterns observed are likely to represent a complex outcome of economic constraints, that is, the costs of production of the scent mark, and the time required to replenish the marks (Gosling & Roberts 2001).

**Table 8.** Overview of scent-marking behaviour in adult and young males (Am and Ym; solitary, nonterritorial with a dominance hierarchy) and female (Af, solitary, mutually exclusive home ranges with overlap) honey badgers and the fit of the results to predictions from four hypotheses on the function of scent marking

Hypotheses and predictions	Type of scent marking					
	Latrines		Squat marking		Token urination	
	Am	Af	Am	Af	Ym	Af
<b>Scent matching</b>						
Dominant/owner marks area to maximize chance marks will be detected	Y	Y	N	N	N	Y
Dominant/owner marks more than subordinates/nonowners	Y	N	N	N	N	N
Dominant/owner marks itself with substance used to mark area	Y	N	Y	N	N	N
Dominant/owner makes itself available for scent matching	Y	N	Y	N	N	N
Dominant/owner removes or replaces marks of other individuals	Y	N	Y	N	N	N
Subordinate or nonowner withdraws from dominant/owner if scent of owner matches scent marks encountered in area	Y	N	Y	N	N	N
<b>Signalling of reproductive status (females)</b>						
Sexual differences in scent-marking behaviour		Y		N		Y
Seasonal changes in female scent-marking rate related to reproductive status		Y		N		N
Females places marks where males are most likely to encounter them		Y		Y		N
Males respond to female marks		Y		Y		N
<b>Spatio-temporal separation (females)</b>						
No seasonal changes in rate of deposition		N		Y		Y
Marking should increase in areas of overlap		N		?		?
Individual is able to determine freshness of mark		Y		Y		Y
Marks placed where neighbouring female is likely to encounter them		N		N		Y
<b>Foraging efficiency</b>						
No sexual differences	N	N	Y	Y	N	N
Marking should occur near foraging area	N	N	N	Y	Y	Y
Marking should occur immediately before, during or after foraging bouts	N	N	N	Y	Y	Y
Marking should increase when resources scarce or patchy	N	N	?	?	N	N
Marks placed where foraging individual is most likely to encounter them	N	N	N	N	Y	Y

Y=evidence for prediction; N=no evidence, ?=insufficient data. Adult males were not observed to use token urination.

### Scent-matching Hypothesis

Neither token urination nor single-use squat marking supports the predictions of the scent-matching hypothesis (Gosling 1982; Table 8). However, the elaborate scent-marking behaviour of males at latrines, the male dominance hierarchy and subsequent encounters between males support all six of the predictions (Table 8). It is likely that the observed hinterland distribution of latrines within the male's home range, with long outreaching arms from a central polygon, maximize the likelihood that a subordinate male honey badger will encounter the scent marks of other individuals (Roberts & Lowen 1997). The lower rate of latrine scent marking in young males and the behaviour of subordinates and dominants during combined visits to latrines suggest that dominant males scent-mark more than subordinates and that marking position is important, although more data are required to test specifically whether marking rate is directly related to social ranking. Since young males move more slowly and shorter distances on a daily basis than adult males (Begg 2001; unpublished data), they may not be able to increase their marking effort because of the increased costs associated with marking behaviour, that is, the extra distances to be covered and the amount of lipid secreted (Kruuk et al. 1984) or may not be able to afford costs associated

with being discovered as a cheat. The neck and belly rub and scratching and rolling behaviours of adult males at latrine sites are likely to impregnate an individual with its own scent and allow for scent matching on later encounters. In addition, while overmarking behaviour was not obvious, 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. Finally, while the scent-matching hypothesis may not be appropriate for most solitary or wide-ranging carnivore species as encounters between competitors are rare (aardwolf, *Proteles cristatus*: Richardson 1991; lion: Funston 1999), encounters between adult male honey badgers are relatively common. Both adult and young males were regularly seen to move around in groups of two to five individuals for up to 3 days at a time (Begg 2001; unpublished data) and on occasion marked at latrines together and actively initiated encounters with other males by following scent found at latrines. The scent-matching hypothesis predicts that, during encounters, low-status individuals should withdraw if the other male's scent matches the dominant smell found at latrines, and high-status individuals should usually withdraw but some encounters should escalate. This prediction is supported by the frequent ritualized agonistic encounters between male honey badgers, where overt aggression is rare

and encounters consist of ritualized intimidation/appeasement behaviour with a predictable outcome based on a dominance hierarchy. On the rare occasions that an individual did not retreat or show appeasement behaviour on an initial encounter, the interaction escalated into aggressive tumbling, biting and chasing, which reinforced the dominance hierarchy (Begg 2001; unpublished data).

#### *Scent matching in females*

The predominant behaviour of females at latrines was not scent marking, but intensive smelling; scent marks were left on less than 50% of all latrine visits. Rich & Hurst (1999) suggested that since scent marks and countermarks of males provide a continuous record of competitive challenges between conspecifics, they provide a reliable advertisement of competitive ability for potential mates. They also suggested that the ultimate function of such competitive signalling may be to provide a signal to third parties. Female honey badgers may use latrine visits for a similar function: to assess the status of males in the area and later match the scent found at latrines with males that approach them for mating. Observations of females during oestrus showed that they appeared reluctant to mate with some males: they left the mating burrow at the first opportunity, ran away, or dug out the back end of the burrow and ran off. However, they 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 (Begg 2001; unpublished data). Odour is clearly not the only factor used by males or females to assess others; more direct signals such as vocalizations and visual signals (e.g. standing tall and piloerection) are also likely to be used in assessment.

#### **Reproductive Advertisement Hypothesis**

While urine is known to contain information about reproductive status and oestrous condition and has been widely associated with advertisement of reproductive condition in other carnivores (Gorman & Trowbridge 1989), in this study token urination did not support the predictions of the reproductive advertisement hypothesis (Table 8). In particular, the lack of any seasonal changes in the rate of token urination or heightened marking frequency by females around oestrus and the observation of token urination in young males precluded this hypothesis as a function of token urination. Latrine scent marking was the only scent-marking behaviour in females that appeared to be associated with the timing of oestrus. The display of flehmen by males at latrines and the fact the males occasionally found females by following their scent from latrines further support this hypothesis (Table 8). However, the low frequency of marking by females during latrine visits suggests that advertisement is not the primary aim (as discussed above). The low level of advertisement of oestrus by female honey badgers may rather be a strategy to avoid mating with or attracting sub-

ordinate males, as has been suggested in the ferret, *Mustela furo* (Clapperton et al. 1988; Clapperton 1989).

#### **Spatiotemporal Separation Hypothesis**

We expected females to use scent marking to maintain spatiotemporal separation (Table 8). Token urination provides support for this hypothesis since it was the only form of scent marking used extensively by females throughout their large home ranges. The observed pattern of scent marks, that is, inner rings with a complex array of outwardly radiating arms, is likely to maximize the chance that a neighbouring female will find the urination marks. Although we did not test the ability of an individual honey badger to assess the freshness of a urination mark, this has been indicated in other carnivores (Macdonald 1985) and there is no reason to suspect that this is not the case in honey badgers. Since female honey badgers do not show a seasonal change in home range size (Begg 2001; unpublished data), the lack of seasonal differences in the rate of token urination further supports this hypothesis. However, the presence of token urination in young males (albeit at a low rate) complicates the issue and could not be easily explained. In addition, the important prediction that token urination would increase in areas of home range overlap could not be tested, as no area of either female's home range was not overlapped by at least one neighbouring female.

#### **Foraging Efficiency Hypothesis**

A related but not mutually exclusive explanation relates token urination to resource dispersion and 'book-keeping' (Henry 1977; Kruuk 1995). Kruuk (1995) suggested that in the European otter, *L. lutra*, sprinting (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 use, which increases foraging efficiency. The timing (during intensive foraging) and position (in foraging holes) of token urination marks appear to support this hypothesis in honey badgers (Table 8).

The foraging hypothesis suggests that a temporal and spatial record of where prey items have already been captured might increase foraging efficiency by reducing the time and energy spent foraging in already used sites (Macdonald 1985; Clapperton 1989; Kruuk 1995) and might therefore diminish competition for undisturbed foraging patches (Koehler et al. 1980; Sillero-Zubiri & Macdonald 1993). It is supported to some extent by the observation that token urination in honey badgers occurred more frequently in holes where prey was successfully captured rather than unsuccessful digging events. However, if it is assumed that the individual is signalling to itself to increase foraging efficiency (Henry 1977) then marking should occur according to stricter rules for it to be effective. In our study, only 34% of successful digging events were marked. Alternatively, if honey badgers are signalling for others, then this implies

a kin-driven system, which is unlikely, particularly since female cubs disperse large distances away from the natal home range (Begg 2001; unpublished data), or reciprocal altruism.

In honey badgers, squat marking is the most difficult scent-marking activity to explain. 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 spatio-temporal separation. Instead, single-use squat marking in both sexes, the significant aggregation of squat-marking sites and the lack of seasonal changes suggest that it is primarily a response to the strong odour of potential resources (mates or food) or potential predators. In terms of valuable resources, single-use squat marking appears to occur under similar conditions to temporary defecation sites. While Ghosh (1981, cited in Macdonald 1985) suggested that similar behaviour in pariah dogs signified ownership, there is no evidence of this in honey badgers as the mark does not prevent other individuals from eating from the same source, for example a solitary bee larvae digging site or sociable weaver nest.

In conclusion, this study emphasizes the importance of direct observations of free-living individuals. While latrines are conspicuous and visual indications of scent-marking behaviour that 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. This study has also shown the importance of visual observations of the behavioural context in which scent marking occurs to understanding its function. A drawback has been the lack of chemical analyses of the scent marks in the honey badger. This might be the next step in unravelling the functional significance of this behaviour.

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