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Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence

NEIL R. JORDAN*†, MICHAEL I. CHERRY* & MARTA B. MANSER‡
*Department of Botany and Zoology, University of Stellenbosch
†Department of Zoology, University of Cambridge
‡Verhaltensbiologie, Zoologisches Institut, Universität Zürich

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Many carnivores defend territories and deposit faeces and other scent marks at specific latrine sites. The role of latrines in territory defence is well established, but evidence suggests at least a subsidiary role in mate defence. We investigated latrine function in cooperative meerkats, *Suricata suricatta*. By analysing the spatial and temporal distribution of latrines we found patterns that might facilitate information transmission to a range of potential intruders. Each group of meerkats usually shared one latrine with each known neighbouring group, which probably allowed efficient intergroup monitoring of surrounding land tenure. The remaining latrines were primarily concentrated in territorial core regions. As transient groups and prospecting males enter territories unpredictably, this distribution may maximize the likelihood of latrine discovery. In large meerkat territories, the chance of intruders missing widely spaced boundary scent marks is high, and a core-marking strategy may therefore be more effective. Latrines were positioned close to refuge sites, which may further increase the likelihood of intercepting intruders, as prospectors are known to visit these sites regularly during intrusions. Although latrine use did not increase during periods when resident females were sexually receptive, it was significantly more likely during the peak breeding period in general, and occurred at significantly greater rates during observation periods when prospecting males were encountered. As prospectors threaten resident male reproductive success, these results highlight the potential importance of latrines in mate defence.

Keywords: carnivore; conflict; latrine distribution; mate defence; meerkat; odour; olfactory communication; scent marking; *Suricata suricatta*; territory defence

Carnivores regularly deposit faeces and other scent marks at specific locations known as latrines (reviewed in Brown & Macdonald 1985; Gorman & Trowbridge 1989). Concentration of these sites along territorial borders in many species suggests that they play a role in territorial defence (sensu Mykytowycz 1968; Thiessen et al. 1968), but the notion that latrines deter intruders from entering occupied areas by forming a kind of 'scent fence' has little empirical support (but see Müller-Schwarze & Heckman 1980). Scent matching is an alternative mechanism, and suggests that intruders assess opponents by comparing scent marks encountered within a territory with either the opponent's scent or a scent mark that it was seen to deposit (Gosling 1982). Because of prior investment made in the territory, owners have more to gain through competitive escalation, and so scent matching facilitates conventional conflict settlement by discouraging costly escalation on the part of the intruder (Parker 1974; Maynard Smith & Parker 1976; Gosling 1982).

Whether latrines function as a scent fence or by facilitating scent matching, territorial owners stand to gain by maximizing the likelihood of intruders detecting their latrines. Although scent marking along the territorial border would seem to be the most effective territorial strategy, activity budget constraints and a limited supply of faeces and scent secretion might make maintaining

Correspondence: N. R. Jordan, Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: nrj26@cam.ac.uk). M. I. Cherry is at the Department of Botany and Zoology, University of Stellenbosch, Private Bag XI, Matieland 7602, South Africa. M. B. Manser is at Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland.

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such a system uneconomical, especially where territory boundaries are relatively long (Gorman 1990). Within the hyaenidae, for example, Gorman & Mills (1984) provided evidence that scent-marking strategies depend on the length of border that must be patrolled by the territory owner(s). Where territorial border length is short relative to the number of patrolling units, latrines are primarily found along the border (e.g. spotted hyaena, *Crocuta crocuta*: Kruuk 1972), whereas species occupying relatively large home ranges adopt a hinterland strategy, scattering latrines and scent marks throughout the territory (e.g. brown hyaena, *Hyaena brunnea*: Mills et al. 1980; Ethiopian wolves, *Canis simensis*: Sillero-Zubiri & Macdonald 1998). In relatively large territories, the chance of intruders missing widely spaced boundary scent marks selects for centrally clustered scent-marking patterns (Gorman 1990), and computer-simulated intrusions show that this marking strategy observed in brown hyaenas is effective in ensuring that intruders detect the signals (Gorman & Mills 1984).

The efficacy of signal transmission may be further increased by strategic positioning on a more local scale which promotes discovery and longevity of signals (Alberts 1992; Bradbury & Vehrenkamp 1998), and many species deposit scent marks on or near conspicuous landmarks such as rocks, trees or crossroads (e.g Iberian wolf, *Canis lupus*: Barja et al. 2004; reviewed in Eisenberg & Kleiman 1972; Macdonald 1985). However, few studies have accounted for the potential nonrandom movement of animals in relation to these features (but see Gilbert 1997 for an exception), and so seemingly selective positioning of scent marks may actually result from a more general affinity for these features.

Alongside their role in territorial demarcation and defence, latrines could play a role in mate defence by advertising the commitment of resident males to defend resident females and deterring neighbouring individuals from entering a territory for mating purposes (Roper et al. 1986). This mate defence hypothesis is based on observed seasonal and sexual differences in latrine use by European badgers, *Meles meles*: males visit boundary latrines more often than females do, and latrine visits peak during the mating season (Kruuk 1978; Pigozzi 1990; Brown 1993; Roper et al. 1993). Seasonal patterns of scent marking and/or latrine use consistent with this hypothesis have been observed in a number of other species (e.g. common otter, *Lutra lutra*: Erlinge 1968; grey wolf, *Canis lupus*: Peters & Mech 1975; North American beaver, *Castor canadensis*: Müller-Schwarze & Heckman 1980; water vole, *Arvicola terrestris*: Woodroffe & Lawton 1990; pine marten, *Martes martes:* Helldin & Lindström 1995).

We investigated whether latrines are involved in mate defence by examining their spatial and temporal distribution in a population of wild meerkats, *Suricata suricatta*. Meerkats are obligate cooperative breeders, living in territorial groups of 2–49 individuals (T. H. Clutton-Brock, unpublished data). Groups usually consist of a dominant breeding pair and their offspring, which remain in their natal group past sexual maturity and help to rear subsequent litters (Doolan & Macdonald 1997; Clutton-Brock et al. 1998b). Subordinates disperse with same-sexed group members at around 18–30 months of age (Clutton-Brock et al. 1998a), and individuals form new (temporarily 'transient') groups with coalitions of unrelated opposite-sex individuals. Alternatively, males may immigrate into an existing group by deposing the resident males after frequent, temporary, 'prospecting' intrusions (Young 2003; Young et al. 2005). If meerkat latrines are involved in mate defence, their spatial and temporal distribution should maximize the likelihood of intercepting these intruding rivals.

Our analyses focused on two main issues. First, by recording the distribution of latrines both in the home range in general and in relation to specific features at a more local level, we determined whether latrines are positioned to promote their discovery and/or longevity. In contrast to previous studies relying on remote methods of observation, we were able to follow our study groups continuously throughout their daily movements, and were therefore able to determine whether any observed nonrandom latrine positioning resulted from nonrandom movement in general. Second, we examined the temporal distribution of latrine use in relation to factors relating to mate defence, focusing on season, encounter events with reproductive rivals and resident female(s) breeding status.

METHODS

Study Site and Animals

We undertook this study between May 2003 and December 2004 on recovering 'ranchland' in the southern Kalahari, 29 km west of Van Zylsrus in South Africa's Northern Cape (28°58′S, 21°49′E, further details in Clutton-Brock et al. 1999b; Russell et al. 2002). The study was carried out under a permit issued by the Northern Cape Conservation Service, South Africa. We collected data from 12 groups of wild meerkats (range in group size 6–25 individuals) habituated to close human observation and handling. To allow rapid individual field identification, we gently applied a small (ca. 1–1.5 cm^2) hair dye (Garnier Nutrisse, L'oréal, Paris, France; Liquorice 1 colour) mark to each individual's pelage with an 8-mm-diameter paintbrush as they stood sunning in the early morning. Meerkats usually did not interrupt this behaviour or investigate these marks, which dried rapidly (<5 min) and were renewed every few weeks.

One individual in each group was also fitted with a radiocollar (Sirtrack, Havelock North, New Zealand) with the transmitter hanging free of the neck by 1 cm at the base and a 15-cm whip antenna protruding over the shoulder. To locate groups we used a Telonics TR-4 receiver (Telonics Inc., Mesa, U.S.A.) attached to a custom-manufactured antenna (Africa Wildlife Tracking, Pretoria, South Africa). Collars weighed 18–22 g ($\bar{X} \pm SD = 2.68 \pm 0.46\%$ body weight, range 1.94–3.74%), and had no discernible effect on survival or foraging ability (K. A. Golabek, N. R. Jordan & T. H. Clutton-Brock, unpublished data). To attach this collar, target adult individuals (>1 year, $N = 24$) were picked up at the tail base during foraging and placed into a cloth bag (75 × 45 cm), where they remained until fully anaesthetized to minimize stress. Individuals were carried to a nearby vehicle (ca. 50 m away), and the group did not respond to the capture or absence of individuals. Through the bag, the captured individual's head was held on either side with the thumb and forefinger, and its nose placed into a small 'gas mask' delivering an initial dose of 4% isoflurane from a car-mounted, specially calibrated vaporizer, using oxygen as a vehicle at a flow rate of 4 litres/min. Isoflurane is a halogenated volatile liquid, which maintains anaesthesia by depressing the central nervous system, and has no effect on fertility, pregnancy or offspring viability in a number of mammals (e.g. mice, *Mus musculus*: Mazze 1985). When fully anaesthetized (after 1–5 min), the individual was removed from the bag, its nose replaced into the mask and the dose was reduced and maintained at 1–2%. The collar was fastened behind the neck with a small bolt, whose flat end lay inside the collar and was covered with shrink-wrap plastic to prevent rubbing. Following collar attachment, isoflurane delivery was ceased, 100% oxygen was supplied for 5 s and the individual was placed into a temperature-controlled, well-ventilated recovery box (90 × 50 × 50 cm) with a sand-covered base. The temperature, heart and breathing rates of captured individuals were monitored throughout each procedure, and individuals regained normal locomotory ability after 1–7 min, but remained in the recovery box for a further 5 min to ensure complete recovery before being released to the centre of the foraging group. After their return, individuals were monitored and usually sniffed the anogenital region of at least one individual before resuming foraging. No dominance change, dominance competition or change in reproductive status occurred as a result of these brief removals, and collars were rotated between individuals every 119.8 ± 62.71 days ($\overline{X} \pm \text{SD}$) following the same capture technique. A total of 47 captures were conducted for collaring during the study period, and some individuals remained collared at the end of the period as the long-term project continued.

We visited groups at least every 3 days during the study to assess group composition and collect behavioural data. We carried out 6221 observation sessions during the study period, the average morning session lasting a mean ± SD of 210 ± 81.2 min ($N = 3367$, range 10–595 min) and afternoon sessions 91 ± 38.3 min ($N = 2854$, range 3–255 min). Observation sessions were distributed approximately evenly between the breeding (49%) and nonbreeding (51%) seasons.

Latrine Description and Classification

Latrine sites contained concentrated accumulations of faeces and were often associated with the deposition of other scent marks. Latrines contained at least two faeces within 1 m of each other, but typically 5–100 or more faeces occurred in an area of 0.5–6 m^2. This area was covered with multiple small pits (about 30 mm in diameter, 10–40 mm deep), which were dug by meerkats during latrine visits. Faeces were scattered individually in and around these pits, and more rarely two to six faeces occurred in a single pit. We assigned latrines to one of three categories based on observed patterns of use during the study: 'singly used latrines' were visited by a single group only once; 'multiply used latrines' were visited by a single group on more than one occasion, and 'shared latrines' were visited by two or more groups at least once.

Spatial Data Collection

We recorded location data with handheld eTrex (Garmin International Inc., Olathe, U.S.A.) Global Positioning System (GPS) units and transferred them into the GIS software program ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). Coordinates were taken whenever groups visited latrines, and group location was recorded every 15 min after the group had left their overnight burrow, continuing until the group reached their next overnight burrow. Observation sessions were divided by a recess coinciding with the midday period of inactivity, and to maximize independence between GPS points, we extracted a single randomly selected coordinate from each observation session. We estimated home ranges and territories from these locations by using the Animal Movement extension in ArcView. To estimate home ranges we used the 95% fixed kernel method (Worton 1989), and we used the least-squares cross-validation (LSCV) value for smoothing, as this provides the least-biased estimates of home range (Seaman et al. 1999). Home ranges were estimated from a mean ± SD of 202.9 ± 36.4 coordinates per group (range 160–260), which is sufficient for kernel analysis (Seaman et al. 1999). Home ranges were further divided into core and border areas. To distinguish between border and core areas, we calculated the percentage of each home range that overlapped with each neighbouring group. We defined neighbours as groups that shared overlapping regions of home range at the 95% kernel, of which there were 14 dyads. The area of each of these overlaps was recorded and individually divided by the 95% kernel area for both groups sharing that overlapping region, and thus converted into a percentage of home range. This was repeated for each kernel size (decreasing by 5% each time). As the 85% kernel approximated the internal boundaries of known range overlap for most groups, this was chosen to divide border and core areas of the home range, and represented the estimated territory boundary. This approach allowed us to estimate overlapping border regions for groups with neighbouring nonstudy groups, whose home ranges could not be estimated. For all groups, the area of the border region was estimated by subtracting the estimated territory area from the estimated home range area. We calculated the densities of latrines in both the border and core areas of the home range for each group by dividing the number of latrines in each region by its area.

Coordinates for each latrine were collected during their first observed use, and they were assigned a unique identification number. The distance to the closest refuge (bolthole or burrow entrance) and tree trunk were recorded for each multiply used latrine site, and for faeces deposited in isolation (not in latrines). All measurements of more than 3 m were taken at crouching height with a handheld rangefinder (Motorola DME Laser 3000A, Motorola, Phoenix, AZ, U.S.A.) (±10 cm), and measurements of less than 3 m were taken with a tape measure (±1 cm). The distance to a refuge was measured to the overhang of the hole.

We located all multiply used latrine sites ($N = 150$) retrospectively by using GPS coordinates. Suitable control sites were located by extracting the next scheduled waypoint recorded after the first observed use of the latrine (i.e. the location of the centre of the group 3–56 min after latrine use; $\overline{X} \pm \text{SD} = 13.05 \pm 8.51$ min). Sample collection at latrine sites took priority, and prolonged latrine use resulted in delays described for control point collection. Unlike randomly plotted control points used in previous studies, these controls allowed us to determine whether any nonrandom latrine positioning we observed was an artefact of general nonrandom movement in relation to the features of interest. Distances were measured from the centre of each latrine and its control site.

To investigate whether meerkat latrines were preferentially positioned close to burrows, we measured the distance to the closest breeding and nonbreeding burrows from each multiply used latrine site. A ‘breeding’ burrow was one used to ‘babysit’ pups for 4 or more consecutive days during the study period, and a ‘nonbreeding burrow’ was any other burrow used for at least 1 night. This definition removed the likelihood of assigning greater significance to nonbreeding burrows, as pups are typically moved to boltholes and minor burrows after abandoned foraging attempts in the latter stages of the babysitting period. Control points were taken for each latrine from the next observation day at the closest time and differed by no more than 30 min. Those latrines where no control point was collected within 14 days were excluded.

To investigate whether faeces were deposited strategically on a local scale, we collected data from meerkats depositing faeces both within latrine sites and in isolation. As the positions of multiple faeces were recorded during each latrine visit, we analysed a single randomly chosen sample from each visit to avoid pseudoreplication. In addition to the standard measurements described above, we recorded whether more than 50% of the individual faeces were in a pit and/or beneath the canopy of vegetation (including trees, shrubs or grass clumps). Corresponding control measurements were taken from the location of the depositing individuals’ tail base 10 min after defecation. The tail base was chosen as a control point as it is a small (ca. 12 mm wide) well-defined point located close to the source of the faeces. Where prolonged latrine use resulted in the control being missed, this was taken the following whole minute after the animal was relocated (range 11–33 min after defecation).

Patterns of Latrine Use

The occurrences of all latrine visits were recorded and examined in relation to temporal and social factors. We classified observation periods by season, the occurrence of intergroup encounters and whether any resident females were in oestrus or whether any prospecting males approached.

Although meerkats have no strict breeding season, successful reproduction is dependent on rainfall, with the vast majority of births occurring in the hot, relatively wet period between October and April (Doolan & Macdonald 1997; Clutton-Brock et al. 1999a). For ease of interpretation we refer to these months as the ‘breeding’ period. The cooler and drier months between May and September result in vastly reduced reproductive activity, and we refer to these months as the ‘nonbreeding’ period. Rates of latrine visits were calculated for the population during the breeding and nonbreeding periods. We determined expected values by assuming that rates of latrine use (the number of latrines used/h that they were observed) remained constant throughout the year. Encounters with other groups and extragroup individuals were recorded ad libitum. Intergroup encounters typically involved a stereotyped threat display or ‘war dance’, with one group usually retreating without physically fighting. Prospecting males commonly approached the edge of the group, and were often and persistently chased off by residents. Although behavioural signs of oestrus are rare, dominant males were observed to mate-guard females by following them closely (<1 m), repeatedly sniffing the anogenital region and chasing away other males who approached. As parturition dates can be accurately determined from dramatic weight loss, and females typically enter oestrous periods between 4 and 12 days postpartum (T. H. Clutton-Brock, unpublished data), additional periods of ‘derived’ oestrus were estimated for the study period. We divided observation periods into nonoestrous periods and those involving the observed oestrus of at least one resident female, and the rate of latrine use for nonoestrous days was compared separately with the rate of latrine use during ‘observed’ and ‘derived’ periods of oestrus.

Statistical Analyses

All statistical tests were carried out in Minitab release 12.21 (Minitab Inc., State College, PA, U.S.A.). We used nonparametric statistical tests throughout, as all data differed significantly from normal (based on the Anderson–Darling test). Results are given as mean ± SE, and all statistical tests were two tailed.

RESULTS

Each group visited 6–24 multiply used latrines (12.5 ± 6.17, $N = 12$) and 17–37 singly used latrines (24.7 ± 2.15) during the study period. Seventeen shared latrine sites were visited, and each group with known overlapping home ranges ($N = 10$) shared at least one latrine with their neighbours (except group ‘ZZ’ whose home range shifted dramatically southwest during the study period).

Spatial Distribution

The mean home range size was 2.06 ± 0.72 km^2 (range 0.91–3.30 km^2, $N = 12$) with a mean perimeter length

(length of the 95% adaptive kernel) of 8.88 ± 0.40 km (range 6.52–11.18 km, $N = 12$; Fig. 1). 'Territory' areas, as estimated by the 85% kernel, had a mean area of 1.08 ± 0.18 km^2 (range 0.31–2.48 km^2, $N = 12$) and a mean perimeter length of 6.08 ± 0.38 km (range 3.13–7.93 km, $N = 12$). Each group with known overlap shared a mean overlapping home range area with each habituated neighbouring group of 0.22 ± 0.096 km^2 (range 0.023–1.43 km^2, $N = 14$ overlapping areas; Fig. 2). Border regions had a mean area of 0.99 ± 0.08 km^2 (range 0.60–1.40 km^2, $N = 12$).

Each group had 4.25 ± 1.0 (range 0–13, $N = 12$) multiply used latrines in the border region of their home range and 4.83 ± 1.0 (range 1–11, $N = 12$) in the core, but these occurred at significantly higher density in the core areas (Wilcoxon signed-ranks test: $T = 6$, $N = 12$, $P = 0.009$). When the border density was artificially increased by including multiply used latrines that occurred outside of the home range, this comparison remained significant ($T = 8$, $N = 12$, $P = 0.017$). Within the 85% kernel (i.e. the territory) multiply used latrines occurred at significantly higher density in core (65% kernel) than in border (between 85 and 65% kernels) areas ($T = 9$, $N = 12$, $P = 0.021$). Each group had 4.75 ± 0.87 (range 0–11, $N = 12$) singly used latrines in the border region of their home range and 6.5 ± 1.13 (range 0–14, $N = 12$) in the core. Singly used latrines occurred at significantly higher densities in the territory core ($T = 3$, $N = 12$, $P = 0.005$).

Latrines were no closer to either a breeding or a nonbreeding burrow than control sites were (Wilcoxon signed-ranks test: breeding burrows: $T = 3842$, $N = 125$, $P = 0.94$; nonbreeding burrows: $T = 3775.5$, $N = 125$, $P = 0.81$), being on average 360.6 ± 26.8 m ($N = 125$; compared to 352.2 ± 26.0 m for their control sites) and 160.5 ± 12.4 m (compared to 158.56 ± 9.26 m for controls) from the closest breeding and nonbreeding burrow, respectively.

Latrines and individual faeces deposited in latrines were significantly closer to a refuge than controls were (Mann–Whitney U test: latrines: $U = 3368.5$, $N_1 = N_2 = 69$, $P < 0.001$; faeces in latrines: $U = 492.0$, $N_1 = N_2 = 27$, $P < 0.001$). Isolated individual faeces were also significantly closer to a refuge than their control sites were ($U = 2517.5$, $N_1 = N_2 = 55$, $P = 0.001$). Neither latrine sites nor individual faeces deposited within latrines or in isolation were closer to trees than their control sites were (latrines: $U = 4612.0$, $N_1 = N_2 = 69$, $P = 0.44$; individual faeces in latrine sites: $U = 859.5$, $N_1 = N_2 = 28$, $P = 0.32$;

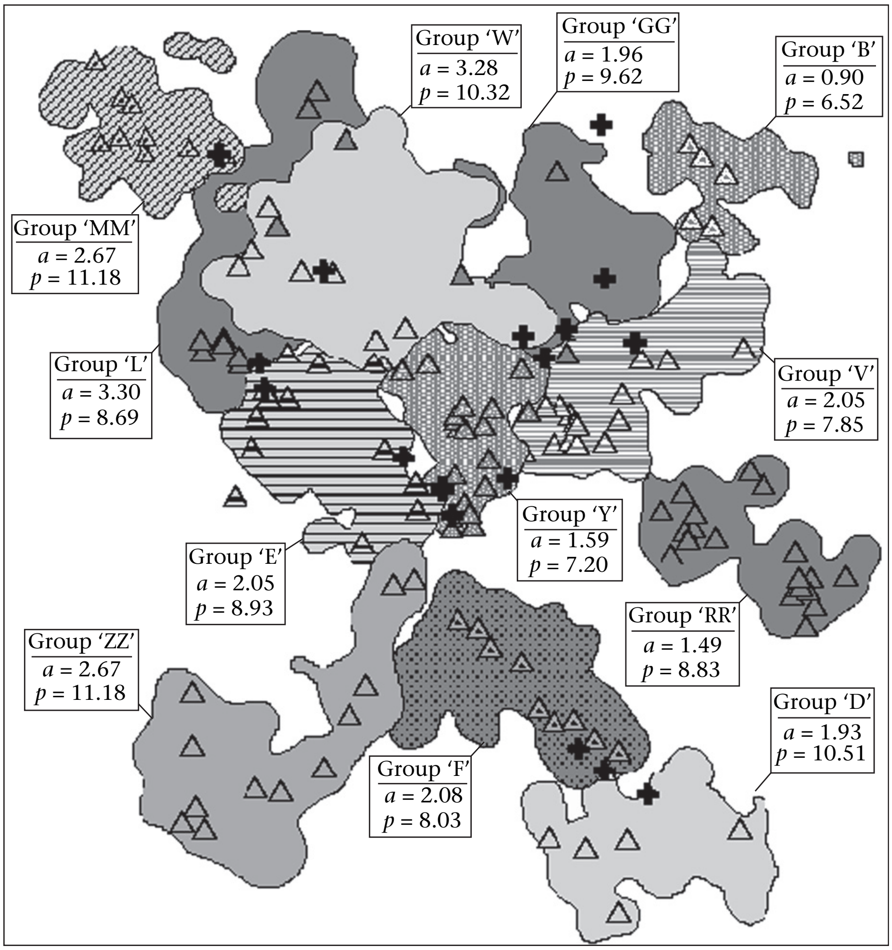

Figure 1. Home ranges for the study population showing all multiply used (△) and shared (✚) latrines. Home range areas (a) in km^2, and perimeter length (p) in km are shown for each group.

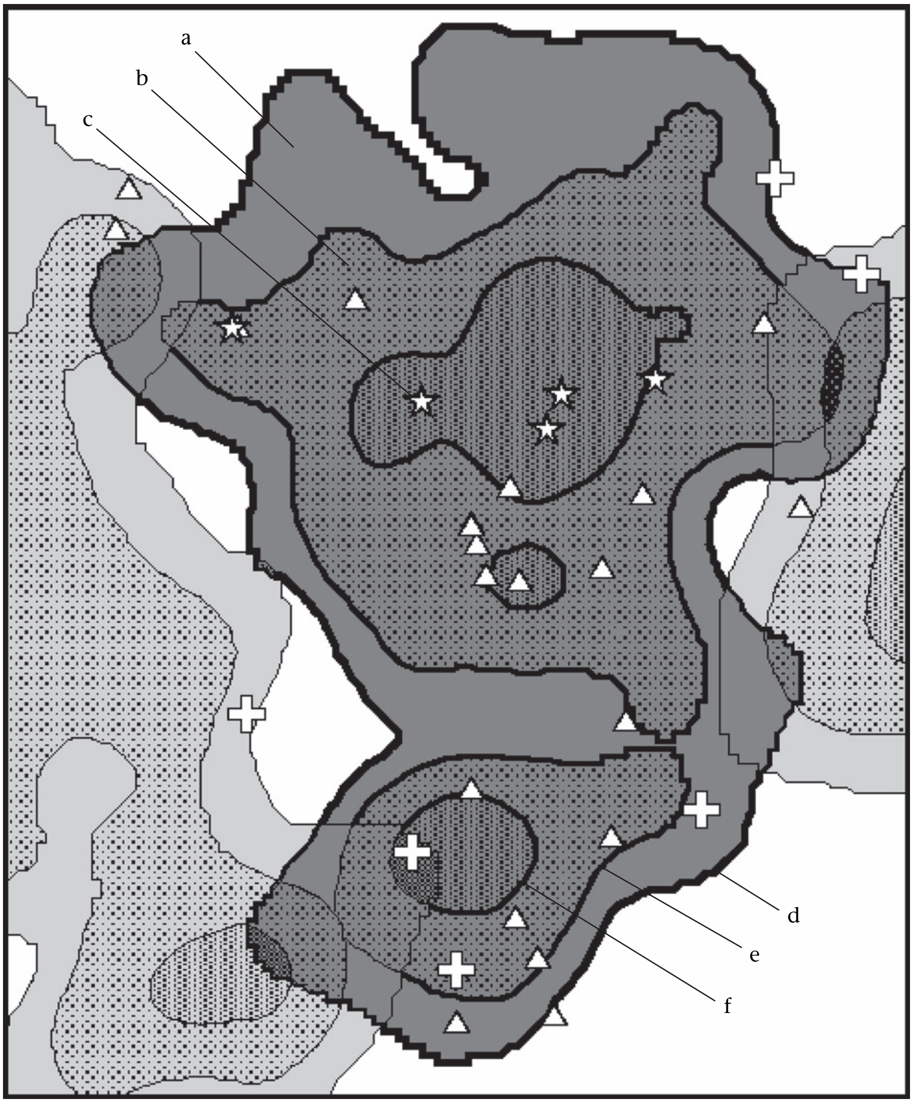

Figure 2. A sample home range for one group showing (a) home range border area, (b) territory border area, (c) territory core area. Areas are divided by (d) 95%, (e) 85% and (f) 65% kernels. Home ranges for two neighbouring groups are plotted in lighter shading. Stars are breeding burrows, crosses are shared latrines and triangles are multiply used latrines.

isolated faeces: $U = 2975.0$, $N_1 = N_2 = 55$, $P = 0.65$). However, significantly more individual faeces deposited in latrines were below the canopy of trees or shrubs than their control points were (chi-square test: $\chi^2_1 = 6.45$, $P = 0.01$), whereas individual faeces deposited in isolation (i.e. not in latrine sites) were no more likely than their controls to be under canopy ($\chi^2_1 = 0.29$, $P = 0.59$). There was no significant difference between latrines and control sites in association with dead trees ($\chi^2_1 = 1.77$, $P > 0.10$), grass ($\chi^2_1 = 1.96$, $P > 0.10$) or shrubs ($\chi^2_1 = 0.47$, $P > 0.30$) but control sites were more likely to have forbs within 2 m than latrines were ($\chi^2_1 = 4.26$, $P < 0.05$).

Patterns of Latrine Use

Latrine use occurred at a significantly greater rate in the breeding period (October–April) than in the nonbreeding period (May–September; chi-square test: $\chi^2_1 = 41.30$, $P < 0.001$) and at a significantly higher rate during observation periods that included at least one encounter with extragroup individuals or another group than during observation periods when no encounter occurred ($\chi^2_1 = 2.51$, $P < 0.001$; Fig. 3). The rate of latrine use was significantly associated with the number of observation sessions that included an encounter with extragroup prospecting males and/or another group throughout the year (Pearson correlation: $r_{17} = 0.820$, $P < 0.001$).

Insufficient data were obtained to assess rates of latrine use during observed oestrous periods, but latrine visits were no more likely to occur during observations covering ‘derived’ periods of oestrus of at least one resident female than during periods when no resident females were in oestrus ($\chi^2_1 = 0.442$, $P = 0.51$). The rate of latrine use was not correlated with the number of conceptions each month (Pearson correlation: $r_{17} = 0.328$, $P = 0.170$; Fig. 4).

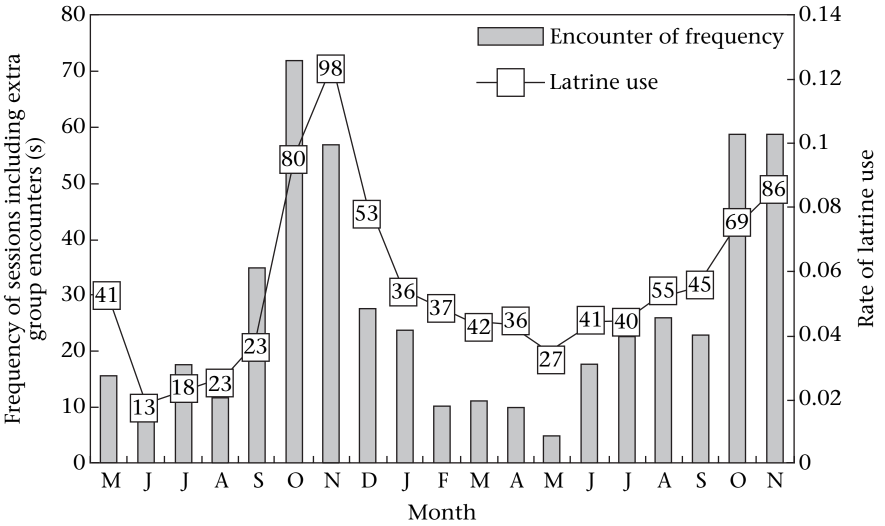

Figure 3. Rate of latrine use (number of visits/h) and the frequency of encounters with extragroup males (number of sessions involving at least one extragroup encounter) throughout the study period ($N = 12$ groups). Numbers given in boxes are the total latrine visits observed in each month.

DISCUSSION

Meerkat latrines were distributed nonrandomly, and patterns were consistent with the hypothesis that latrines may serve to maximize the likelihood of intercepting intruders on the territory. As meerkat territorial residents may encounter three broad types of intruder which vary both in predictability and threat, the overall observed scent-marking strategy adopted may reflect the different selection pressures resulting from this diversity.

Differential responses by residents according to intruder type are a common phenomenon (reviewed by Temeles 1994), with individuals of many species responding more aggressively to strangers than to neighbours (e.g. northern harriers, *Circus cyaneus*: Temeles 1989a, b; green woodhoopoe, *Phoeniculus purpureus*: Radford 2005). This 'dear enemy' phenomenon may result from the differential threats presented by neighbours and strangers (Temeles 1994), and could explain the system of shared latrine sites we observed in meerkats. As neighbouring groups encroach from predictable directions and threaten a permanent loss of space (Gosling 1987), shared latrine sites presumably facilitate efficient intergroup monitoring. Prolonged territorial border disputes with neighbours would be deleterious and are therefore often settled by convention (Parker 1974). As visual encounters with neighbouring groups usually result in costly chases, and may escalate to physical fights (Young 2003), it is possible that such a system of shared latrine sites facilitates intergroup information transfer and allows economical monitoring of land tenure in the surrounding territories. However, it is probable that such a stalemate will be maintained only while the participants respect the established borders, and that if latrine translocation experiments were used to simulate

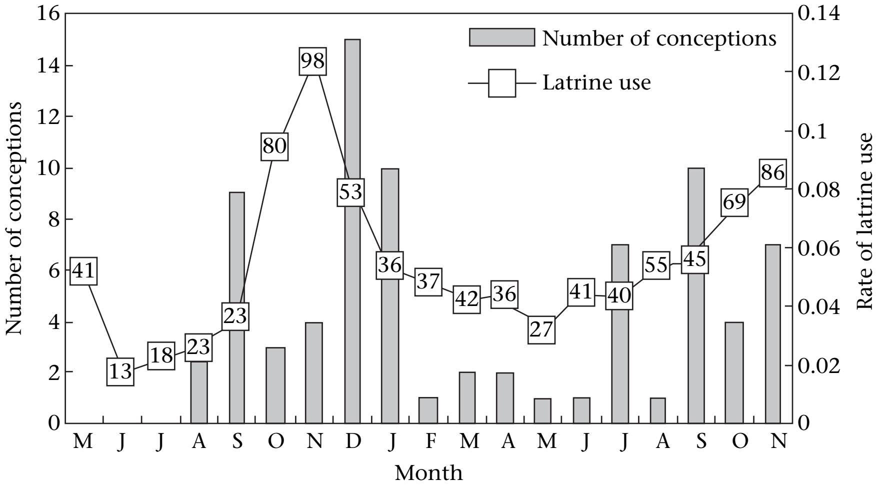

Figure 4. Rate of latrine use (number of visits/h) and the total number of conceptions throughout the study period ($N = 12$ groups). Numbers given in boxes are the total latrine visits observed in each month.

territorial invasion, elevated responses might be seen. This has recently been shown in banded mongooses, *Mungos mungo*, where resident groups responded more strongly to a neighbouring group's latrine than to a strange group's latrine when latrines were created experimentally within the recipient group's territory (Müller & Manser 2007). In addition, territorial animals respond quickly to changes in the movement patterns or disappearance of neighbours by expanding their own range (e.g. red fox, *Vulpes vulpes*: Macdonald 1977; reviewed in Kruuk & Macdonald 1985), and meerkats may similarly monitor shared latrine sites and respond to neighbouring group movement by enlarging their own territory, or even making temporary intrusions when neighbours are elsewhere.

In contrast to neighbouring groups, extragroup prospecting males and transient groups may enter the territory from any direction, and often cross multiple territories during forays (Young 2003): transient groups threaten a severe loss of space, potentially taking over the entire territory, while prospecting males threaten the dominant male with permanent takeover or loss of paternity. Meerkat latrines occurred at significantly higher densities in the core than the border regions of home ranges, and this 'core-marking strategy' contrasts with that of many carnivores living in high-density populations, which commonly concentrate their scent marks on or close to territorial borders (e.g. European badgers: Kruuk 1978; Pigozzi 1990; Brown 1993; Roper et al. 1993). However, a core-marking strategy is also adopted by honey badgers, *Mellivora capensis* (Begg et al. 2003, 2005) and brown hyaenas (Mills et al. 1980) living in extremely large home ranges in a similar habitat in the southern Kalahari. This suggests that a border-marking strategy may be economically feasible only in high-density populations, because of the complementary effects of decreasing border length and an increase in the number of individuals contributing to its maintenance (Macdonald 1985; Gorman 1990), which is consistent with data from the hyaenidae showing that in populations where individual patrolling units would have to travel greater than about 7.5 km to mark their border, scent marks are distributed throughout the home range (Gorman & Mills 1984). Given the length of meerkat home range (8.9 km) and territory (6.1 km) perimeters, and the constraint that groups must travel together and 'maintain' their latrines as a single unit, it is probably not economically feasible for meerkats to maintain an effectively marked perimeter against unpredictable intruders.

Strategic positioning of meerkat latrines and faeces also occurred on a more local level and, in common with latrine and faeces distributions in other mammalian species (e.g. Iberian wolf: Barja et al. 2004, 2005), may assist in increasing signal persistence and further maximizing the chance of signal discovery (e.g. Roberts 1997; Roberts & Lowen 1997; reviewed in Macdonald 1985). In contrast to Eurasian beaver, *Castor fiber*, where transients enter territories in predictable locations, and residents concentrate their scent marks at these sites (Rosell et al. 1998), meerkat intruders may enter the territory from any direction, and consequently strategic positioning, if it occurs, may be more subtle in this species. Accordingly, meerkat latrines and faeces deposited in isolation were significantly closer to a refuge site than their control sites were, and as prospecting males spend long periods inspecting refuge sites and burrow systems (Doolan & Macdonald 1996), meerkats may increase the likelihood of latrines being discovered by intruders by selectively placing them close to a refuge. However, one could argue that such a result may be explained by the general tendency of meerkats to remain close to a refuge (Manser & Bell 2004). As we were able to follow our study animals closely, however, we were also able to collect control points from the group a given time after they had visited a latrine. Our results show that although meerkats generally remained close to a refuge, they placed their latrines significantly closer to latrines than they themselves generally were, which supports the conclusion that latrines are selectively positioned close to a refuge. This method is an improvement on the approach of previous studies on other species where random control points were (necessarily) used (e.g. European badger: Stewart et al. 2002), and which therefore could not account for any bias in the general movement of their study species. As latrines were no closer to burrows than control sites were, the proximity of latrines to a refuge cannot be explained by a tendency to deposit latrines close to sleeping or breeding burrows. Additional selective positioning may further increase the efficacy of signals by promoting their protection and longevity (Alberts 1992), and although we did not explicitly test whether nonrandom positioning increased signal longevity, it seems reasonable to suggest that signals from meerkat faeces that are deposited under the canopy of trees, close to vegetation and in pits will last longer than those exposed on the surface.

Meerkats visited latrines throughout the year, but rates of latrine use were highest in the breeding period from October to April inclusive. This is consistent with other species where observations were also made throughout the year and showed that scent marking (e.g. common otter: Erlinge 1968; grey wolf: Peters & Mech 1975; pine marten: Helldin & Lindström 1995; European badgers: Buesching & Macdonald 2004) and latrine use (e.g. European badgers: Neal 1977; Kruuk 1978; Roper et al. 1986; Brown et al. 1992; Stewart et al. 2002) increased to a peak during the mating season. By defending a territory, males may be attempting to prevent neighbours from gaining reproductive access to resident females (e.g. Lack 1966; Wrangham 1982), and our data on the temporal patterns of latrine use provide at least circumstantial support for the hypothesis that latrines advertise the commitment of resident males to defend resident females (Roper et al. 1986). In addition to increased rates of latrine use during the breeding season, meerkat groups also visited latrines at greater rates during observation periods when they encountered extragroup males than during those when no encounter occurred, and monthly rates of encounters with extragroup males were significantly correlated with monthly rates of latrine use. Indeed, groups often ran specifically to latrine sites in response to the arrival of prospecting males, and these sites were frequently investigated by these males after the group had retreated (personal observation). Although latrine visits did not occur at higher rates during observation periods when at least one resident female was sexually receptive, it is possible that a weak effect exists that is masked by our method of data collection. Unfortunately there were not enough cases of observed oestrus for analysis, and so we back-dated from birth dates to estimate periods of postpartum oestrus for females. Although observed oestrous periods lasted only about 3 days (personal observation), our derived oestrous periods covered the entire 8 days of potential oestrus, meaning that any small effect could have been diluted by the relatively large number of non-oestrous days included in the sample.

We conclude that both the spatial and temporal distributions of meerkat latrines are consistent with a role in territory defence, and suggest that latrines may also fulfil an important role in mate defence. Whereas the observed system of latrines shared between groups may facilitate intergroup monitoring, groups may effectively intercept intruding males by concentrating their exclusive latrines within the territorial core and close to refuge sites (which intruders visit). Finally, meerkat groups visited latrines more frequently during the peak breeding period, and during observation sessions when encounters with extra-group males occurred. Although further work on individual behaviour at latrine sites, and the response of intruders to these sites, is necessary, these results suggest that meerkat latrines may fulfil an additional role in mate defence.

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