



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

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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.

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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

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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 depositing 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 cm²) 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 ($\bar{X} \pm \text{SD} = 2.68 \pm 0.46\%$ 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

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