Meerkat latrines: cooperation, competition and discrimination

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Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: Date: ***09 September 2005***

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Summary

Many territorial carnivores deposit faeces and other scent-marks at specific latrine sites, and their role in territorial defence is often assumed. However, recent empirical and theoretical work suggests that ultimate explanations of territoriality differ between the sexes. In this thesis, I investigate patterns of latrine-use in cooperatively breeding meerkats, *Suricata suricatta*. Meerkats exhibit high reproductive skew, and in such societies an individual's optimal investment in territory defence and intruder deterrence will depend not only on its sex, but also its breeding status within the group. The spatial and temporal distribution of meerkat latrines reflects the diversity in intruder type. Shared latrine sites between neighbouring groups facilitate cost-effective monitoring of predictable intruders and surrounding land tenure. In contrast, intruding transient groups and prospecting males are effectively intercepted by latrines concentrated in the core of the territories, close to refuges. This represents the optimal strategy, as meerkat territories are too large to allow effective scent-marking around their entire peripheries, and these intruders travel between refuges during intrusions. Temporal patterns of latrine-use suggest their importance in mate-defence. Latrine-use was correlated with encounters with prospecting males and oestrous periods of resident females, and reached a peak coinciding with the season of elevated dispersal and take-over events. Additionally, rather than cooperatively contributing to territorial defence, individuals participated selfishly at latrines. Males preferentially over-marked female scent-marks and scent-marked at significantly greater rates than females, which resulted in male-biased latrines that were unrepresentative of group composition. Although all individuals investigated female scent-marks for significantly longer than male scent-marks, females invested most, suggesting that intra-group monitoring is an important aspect of latrine visits for females. The deleterious effects of close inbreeding are well known, but regular dispersal in both sexes, and long dominance tenure, result in unfamiliar siblings having a high probability of encountering one another post-dispersal. As latrines are implicated in mate-defence, olfactory assessment of factors affecting mating decisions might be expected, but although individuals do recognise foreign faeces, discrimination does not appear to occur on the basis of kinship. Together, these findings have broad implications for our understanding of individual variation and sex differences in scent-marking behaviour and territoriality.

Opsomming

Baie territoriale karnivore deponeer faeces en ander reukmerke by spesifieke latrines en die latrines se rol in gebiedsverdediging word dikwels aangeneem. Onlangse empiriese en teoretiese werk stel egter voor dat die uiteindelike verduidelikings van territorialiteit verskil tussen die geslagte. In hierdie tesis ondersoek ek patrone van latrine-gebruik in samewerkend-broeiende meerkaaie (*Suricata suricatta*). Meerkaaie toon ‘n hoë graad van voorkeuraanwas en in sulke gemeenskappe sal ‘n individu se optimale belegging in gebiedsverdediging en indringer-verjaging nie net van sy/haar geslag afhang nie, maar ook van sy/ haar teelstatus in die groep. Die ruimtelike en temporale verspreiding van meerkat latrines weerspieël die verskeidenheid van indringertipes. Gedeelde latrine areas tussen naburige groepe help die koste-effektiewe bestekopname van voorspelbare indringers en omringende landsbesetting aan. In kontras hiermee word tydelike groepe en geleentheidsoekende mannetjies effektiewelik voorgekeer deur latrines wat gekonsentreer is in gebiedskerne, naby aan skuilplekke. Dit verteenwoordig die optimale strategie, aangesien meerkat territoriums te groot is om effektiewe reukmerking van die hele grens toe te laat, en synde hierdie indringers tussen skuilplekke reis tydens invalle. Tydspatrone van latrine-gebruik dui die belangrikheid hiervan in paarmaat-beskerming aan. Latrine-gebruik korreleer met ontmoetings met geleentheidsoekende mannetjies en die oestrus tydperk van inwonende wyfies, en bereik ‘n toppunt tydens die seisoen van verhoogde verspreiding en oornames. Ook sal individue selfsugtig deelneem by latrines eerder as om samewerkend by te dra tot gebiedsverdediging. Mannetjies verkies om vroulike reukmerke oor te merk en reukmerk teen ‘n beduidend hoër koers as wyfies, wat lei tot mannetjie-geneigde latrines wat nie verteenwoordigend is van die groepsamestelling nie. Alhoewel alle individue vroulike reukmerke beduidend langer as manlike reukmerke ondersoek, belê wyfies die meeste, wat daarop dui dat intra-groep monitering ‘n belangrike aspek van latrine-besoeke is vir wyfies. Die nadelige effekte van sterk inteling is goed bekend, maar gereelde verspreiding in beide geslagte en lang dominante posisiehouding lei daartoe dat daar ‘n groot kans is vir onbekende nabye familielede om mekaar te ontmoet na verspreiding. Aangesien latrines ‘n rol speel in paarmaat-verdediging kan dit verwag word dat daar olfaktoriese beoordeling sal wees van faktore wat paringsbesluite beïnvloed, maar hoewel individue wel vreemdelinge se faeces herken, toon hulle geen onderskeidingsvermoë gebaseer op verwantskap nie. Saamgevoeg, het hierdie bevindinge wye implikasies vir ons begrip van individuele variasie en geslagsverskille in reukmerk-gedrag en terriorialiteit.

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1

General Introduction

1.1 Olfactory communication and discrimination

Communication can be defined as the transfer of information via signals to the mutual benefit of sender and receiver (Marler 1977; Markl 1985; Dusenbury 1992). The main types of communication employed are visual, acoustic, olfactory, and tactile and although different groups of animals rely on different sensory channels for communication, species generally specialise in one or a few of these sensory modalities (Krebs & Davies 1993). In mammals, odours are a primary mediator of signals (Brown & Macdonald 1985), and they are important in a number of aspects of their daily lives (for general reviews on the function of scent-marks see Kleiman 1966; Brown 1979; Macdonald 1980, 1985; Gorman & Trowbridge 1989).

Scent-marking is the active deposition of glandular secretions or eliminate into the environment, and although difficult to quantify, can be an energetically expensive exercise (Gosling et al. 2000). As scent-marking may involve significant investments in both time and energy, individuals increase the efficiency of signal transfer by depositing scent-marks in specific locations which maximise their chances of discovery by the intended recipient(s) (Gorman & Trowbridge 1989). In many instances, faeces and urine are included in discussions of scent-marks, fulfilling Kleiman’s (1966) criteria of being (a) repeated frequently on the same object or in the same location, (b) elicited by familiar landmarks and novel objects or odours, and (c) often oriented to specific objects (for a review of the use of faeces and urine in carnivore communities see Macdonald 1980). This is further justified, as in many species it is possible to determine the sex and reproductive status of individuals by quantifying metabolites of sex-steroids excreted in faeces and/or urine (Heisterman et al. 1995), and most female terrestrial mammals transmit information about reproductive condition chemically (Eisenberg & Kleiman 1972; Epple 1986; Ziegler et al. 1993; Converse et al. 1995). Furthermore, several carnivores use urine and or faeces as reliable advertisement signals in the context of reproduction (Brown & Macdonald 1985).

In order for scent-marks to function effectively as signals, a degree of olfactory discrimination is required. Discrimination is the process of reliably assigning stimuli into one of a number of categories, and members of a wide variety of mammalian species have been shown to discriminate scents according to biologically important criteria. Various carnivores are able to discriminate scent-marks on the basis of group membership (e.g. raccoon dog, *Nyctereutes procyonoides,* Yamamoto 1984; European badger, *Meles meles,* Davies et al. 1988), sex (e.g. domestic dog, *Canis familiaris,* Dunbar 1977; meerkat, Gsell 2002), and even individual identity (e.g. Indian mongoose, *Herpestes auropunctatus,* Gorman 1976; brown hyaena, *Hyaena brunnea,* Mills et al. 1980; European badger, Kruuk et al. 1984; Christian 1993). In some species, although the discriminatory ability of individuals in response to different scents has not been empirically tested, the chemical composition of scent-marks differed consistently across these categories. For example, analytical studies based on gas-chromatography show that sub-caudal secretions from European badgers have inter-group and inter-individual differences in their chemical profile (Gorman et al. 1984), and these profiles are sex and season specific (Buesching et al. 2002). Although Kruuk and colleagues (Kruuk et al. 1984) showed that captive badgers were able to discriminate between individual scents, whether this is possible in the field remains unclear. Additionally, Sokolov et al. (1984) demonstrated that bank vole, *Clethrionomys glareolus,* faeces carry information on stable characters such as species, sex and age, whereas urine, in addition to carrying information on these factors, also codes for rapidly changing physiological information such as stress and oestrous. Such abilities have various advantages in many aspects of social life.

1.2 Latrines and their phylogenetic distribution

Latrines are accumulations of faeces resulting from repeated utilisation of specific locations for defecation. Such sites are often associated with the deposition of glandular secretions or visually conspicuous marks such as scratches (Macdonald 1980). The use of latrine or ‘midden’ sites has been documented throughout the Class Mammalia, and includes examples from primates (Irwin et al. 2004), ungulates (Leuthold 1977; Estes 1991), rodents (e.g. water vole, *Arvicola terrestris*, Woodroffe & Lawton 1990), lagomorphs (European wild rabbit, *Oryctolagus cuniculus*, Sneddon 1991), and even marsupials (Spotted-tailed quoll, *Dasyutus maculates,* Kruuk & Jarman 1995). Despite a conspicuous absence of latrine-use in the Ursidae, and relatively low occurrence in the Felidae, latrine-use is probably most widespread and intensively studied in the Carnivora (see Table 1.1). Within this order, published evidence of latrine-use exists for at least 25 species across eight families.

Table 1.1: Species from the Order Carnivora where latrine-use has been documented.

Family	**Common name**	**Species name**	**References**
Canidae	Ethiopian wolf	*Canis simensis*	Sillero-Zubiri & Macdonald 1998
	Coyote	*Canis latrans*	Camenzind 1978 Ozaga & Harger 1966 Ralls & Smith 2004
	Kit fox	*Vulpes macrotis mutica*	Ralls & Smith 2004
	Grey fox	*Urocyon inereoargenteus*	Trapp 1978
	Dhole	*Cuon alpinus*	Malcolm (personal communication in Macdonald 1980)
	Golden jackal	*Canis aureus*	Macdonald 1979
	Maned wolf	*Chrysocyon brachyurus*	Kleiman 1972
	Raccoon dog	*Nyctereutes procyonoides*	Yamamoto 1984
Mustelidae	European badger	*Meles meles,*	Kruuk 1978
	Honey badger	*Mellivora capensis*	Begg et al. 2003
	Pine Marten	*Martes Martes*	Lockie 1966
	Common otter	*Lutra lutra*	Kruuk & Hewson 1978
	Striped weasel	*Poecilogale albinucha*	Alexander & Ewer 1959
Herpestidae	Meerkat	*Suricata suricatta*	Ewer 1963
	Dwarf mongoose	*Helogale parvula*	Rasa 1977
	Long-nosed mongoose	*Crossarchus alexandri*	Kingdon 1978
Hyaenidae	Spotted hyaena	*Crocuta crocuta*	Kruuk 1972
	Brown hyaena	*Hyaena brunnea*	Mills et al. 1980
	Striped hyaena	*Hyaena hyaena*	Macdonald 1978
Protelinae	Aardwolf	*Proteles cristatus*	Nel & Bothma 1983 Kruuk & Sands 1972
Viverridae	African civet	*Civettictis civetta*	Bearder & Randal 1978
	Palm civet	*Paradoxurus hermaphroditus*	Bartels 1964
Felidae	Feral cat	*Felis catus*	Molsher 1999
	Bobcat	*Lynx rufus*	Bailey 1974
Procyonidae	Raccoon	*Procyon lotor*	Page & Swihart 1998

However, despite a relatively detailed knowledge of the phylogenetic distribution of latrines, patterns of latrine-use and behaviour at latrine sites is relatively poorly known, which detracts markedly from our understanding of the function of latrines and scent-marking in general.

1.3 Proposed function(s) of latrines

As many species produce composite latrines with faeces, urine and other scent-marks deposited together, the role of latrines in communication is generally accepted. Within this general framework however, there are a number of competing hypotheses for the function of latrines. Many of these hypotheses are not mutually exclusive, but they can be split into two general categories depending on whether or not they involve the defence of resources.

1.3.1 Resource defence hypotheses

The defence of four main resources are commonly cited as proposed functions for latrine or scent-marking behaviour in general. The most commonly supposed defended resource is the territory *per se*, and others are the resources that are commonly contained within most all-purpose territories: food sources, mates, and sleeping or breeding sites. I will now consider each in turn, and review existing evidence that latrines function in the defence of each resource.

Territory

Territories are fixed areas from which residents exclude intruders by some combination of advertisement, threat and attack (Kaufmann 1983), and ever since Hediger's (1949) original contribution, scent-marking has generally been assumed to fulfil a territorial role similar to that of avian song. If latrines are a method of demarcating a territory, it is expected that most be placed along territorial borders (Johnson 1973), and there are indeed many examples of boundary deposition of faeces in carnivores (e.g. European badger, Kruuk 1978; golden jackal, *Canis aureus*, Macdonald 1979; spotted hyaena, *Crocuta crocuta,* Gorman & Mills 1984). However, Macdonald (1980) suggested that only group-living species can produce enough faeces to maintain border latrines, and gave examples of many social and solitary species that do not scent-mark along their territory borders but do so throughout their home range instead. Indeed, mammals seem to scent-mark throughout their territory where regularly patrolling and maintaining a set of border latrines is economically unfeasible (e.g. Gorman & Mills 1984; Gorman 1990). Gorman & Mills (1984) discussed this hypothesis within the hyaenidae, and suggested that both inter- and intra-specific variation in latrine (and scent-mark) location occurs in relation to economic and ecological constraints. All three species of extant hyaena and the closely related aardwolf, *Proteles cristatus*, use latrine sites, and paste-mark grass stems with a substance excreted from the anal pouch. Generally those species with relatively large home ranges (e.g. brown hyaena, Mills et al. 1980) scent-mark throughout the territory, whereas those in smaller ranges mark the border (e.g. spotted hyaena, Kruuk 1972). While border marking gives the earliest warning of transgression, it involves only a single line of defence, which must be relatively continuous and well maintained to ensure that intruders do not pass through without detecting it. This clearly requires the production of a large volume of scent, and regular patrols to distribute it around the border, which is not economically feasible where the length of territorial border that must be patrolled by individuals is large. Although all hyaena species seem to fit this economically driven pattern of latrine distribution, intra-specific variation in spotted hyaena latrine distribution perhaps provides the best illustration. In the Ngorongoro Crater, where an abundant food supply supports large groups in small territories, hyaena position most latrines along territorial borders (Kruuk 1972). In contrast, small groups of spotted hyaena occupy large home ranges in the Kalahari desert where they adopt a ‘hinterland’ marking strategy, positioning latrines throughout their territory (Mills & Gorman 1987).

The traditional interpretation of latrines and scent-marks is that they formed a kind of “scent fence”, representing a “keep out” message against intruders (e.g. Hediger 1949). However, such an effect has only been convincingly demonstrated in two species, the North American beaver (Müller-Schwarze & Heckman 1980) and the blind-mole-rat, *Spalax ehrenbergh* (Zuri et al. 1997), which contrasts markedly with numerous observations of territorial intrusions by non-resident individuals from many species (e.g. dwarf mongoose, *Helogale parvula,* Rood 1983; African lion, *Panthera leo*, McComb et al. 1994; meerkat, Doolan & Macdonald 1996). In fact, Sun & Müller-Schwarze (1998) later demonstrated experimentally that beaver responses to alien scent-marks are inconsistent with a scent-fence effect.

The failure of the scent-fence hypothesis does not necessarily contradict the role of latrines in territory defence. Gosling (1982) realised this and, in reassessing the function of scent-marks in territories, proposed an alternative mechanism. Although territorial intrusions are relatively common, direct fights between territory owners and intruders are relatively rare with disputes usually settled by convention on the basis of property tenure, with the intruder retreating (e.g. Gosling & McKay 1990). However, in order to conventionally settle disputes of this type, the intruder must unambiguously recognise the owner and, as direct contact between opponents is potentially dangerous, long-lasting olfactory cues would seem ideal for this purpose. When intruders and owners meet, an asymmetry of contest is established. By comparing the potential owner’s scent - or a scent-mark that it is seen to have made - with scent-marks encountered within the territory, intruders may unambiguously identify the owner and retreat. As only a long-term resident will have been able to fill his territory with scent-marks, this may provide a reliable and honest signal of ownership. As territory owners have already made significant investments in the territory, it pays the owner more to defend the territory than it does the intruder to escalate the conflict in a take-over bid (Maynard-Smith & Parker 1976; Hammerstein 1981; Gosling 1982) as supposed by the payoff asymmetry hypothesis (Dawkins & Krebs 1978; Krebs 1982).

Animals do not defend territories for space alone, but for the resources that these sites contain. As the motivation for territoriality may differ between the sexes (e.g. African lion, Pusey & Packer 1997; Spotted hyaena, Boydston et al. 2001) so may the motivation for latrine-use. Falling under the umbrella of resources potentially defended by latrine-use are food sources, sleeping and breeding sites, and mates, and each are considered below.

Food sources

The spatial association of latrines with food resources has been recorded for some species. For example, striped hyaena, *Hyena hyaena*, latrines occur close to feeding areas (Macdonald 1978), concentrations of faeces around fruiting trees are described in the grey fox, *Urocyon inereoargenteus* (Trapp 1978), and spotted hyaena in some populations form temporary latrines close to large kills (Bearder & Randall 1978). However, in many species the prey or consumable vegetation is uniformly or cryptically distributed making comparisons or conclusions difficult to make. An alternative explanation for the association of latrines close to feeding sites is that they signal resource depletion. Where individuals den together but forage individually or in small groups (such as spotted hyaena, European badger, and Ethiopian wolf, *Canis simensis*), latrine-activity may signal resource depletion to the mutual benefit of all group members. As European badgers tend to deposit faeces in latrines immediately prior, during and after feeding bouts, faeces volume at latrine sites could effectively signal resource depletion and maximise foraging efficiency for group members (Kruuk 1992; Stewart et al. 2001). Furthermore faeces volume and consistency are likely to be honest signals of the type and richness of resources exploited (Buesching & Macdonald 2001), as they vary considerably in appearance and consistency according to diet (Kruuk 1989), and the fact that boundary latrines are located on the food-isopleths between neighbouring groups suggests at a least a potential role in signalling resource depletion (Stewart et al. 1997). Finally, common otter, *Lutra lutra*, latrines are not associated with territorial boundaries, but instead are interpreted as functioning in the spacing of foraging individuals within group territories (Kruuk 1992).

Although it is possible that latrine-use and scent-marking in general have different functions even within the same species, some evidence concordant with the resource depletion hypothesis exists from non-latrine scent-marking patterns. Marmosets, *Callithrix spp.* (Lacher et al. 1981; Rylands 1985), and African palm civets, *Nandinia binotata* (Charles-Dominique 1978), scent-mark the trees from which they feed, and European foxes, *Vulpes vulpes,* urine-mark depleted caches (Henry 1977). In the latter case it is possible that such marking could reduce the time invested in subsequent investigation of these sites. However, since the visual effects of prior cache retrieval are probably obvious from a distance, it is unlikely that this functions in signalling resource depletion. Instead, foxes may use the conspicuous sites to promote urine detection by conspecifics.

Breeding and sleeping site(s)

Latrines (“scats”) of coastal common otters were more than twice as numerous within 100 metres of holts than elsewhere (Kruuk & Hewson 1978). However, as the route of otters into their holts is determined by landing points along the water’s edge, otters probably only need to mark these regions, as all other resources are under water. Ewer (1963) suggested that meerkat latrines are most often found close to dens, but her study was based on a captive population where movement away from the burrow was restricted. Additionally, burrow-based latrines are also reported for the sympatric yellow mongoose, where latrines are often located at burrow entrances (Le Roux personal communication). Again, further evidence from European badgers supports the hypothesis that some latrines at least may also function to advertise a commitment to defend sleeping or breeding sites (see Buesching & Macdonald 2004).

Mates

Strategies for maximising reproductive success are sexually dimorphic in most mammals, with mates generally representing a more limiting resource for males than for females (Trivers 1972; Clutton-Brock 1988). Various authors have suggested that territoriality is a mechanism for deterring kleptogamy, in that by defending a territory males attempt to prevent neighbours from gaining reproductive access to resident females (e.g. Lack 1966; Wrangham 1982; Roper et al. 1986). In accordance with this hypothesis, sex- and seasonal-biased differences in the use of boundary latrines by European badgers is interpreted as at least partially demonstrating that they function in mate-defence by deterring males from entering occupied territories for mating purposes (Brown et al. 1992; Roper et al. 1993; Stewart et al. 2002). Territorial defence in badgers, in the form of overt aggression and latrine-use, shows a seasonal peak in early spring, which coincides with peak mating activity (Neal 1977; Kruuk 1978; Roper et al. 1986; Buesching & Macdonald 2004). However, the strength of any correlation between latrine-use and mate-defence is not known (Roper et al. 1986).

Sillero-Zubiri & Macdonald (1998) suggested a similar hypothesis for the defence of mates in Ethiopian wolves, and investigated the seasonal, sexual and dominance patterns of general scent-marking rates in this species. Female Ethiopian wolves seek copulations with males from neighbouring packs along territorial borders (Sillero-Zubiri et al. 1996) and may engage in extra-territorial forays (Sillero-Zubiri & Gottelli 1995). Resident females chase these intruders away but males do not, thus the authors suggest that these ‘floater’ females probably use the demographic information contained within scent-marking sites to determine whether a breeding position is available, but no direct evidence of such a mechanism exists in any species. Finally, water vole latrines are not maintained outside the breeding season, and Woodroffe & Lawton (1990) suggest that they signal sexual receptivity. This is the only study to point to this function for mammalian latrines, but unfortunately is based on sparse evidence.

1.3.2 Non-resource defence hypotheses

Parasite reduction

Red howling monkeys, *Alouatta seniculus,* use specific sites for defecation, which are characterised by areas free of underlying vegetation (Gilbert 1997). This is interpreted as an adaptation to decrease the likelihood of contaminating potential food sources or arboreal pathways, and seems the most likely conclusion for the function of latrine-use by primates (including humans) in general. Although reports of latrine-use are relatively uncommon for primates (but for a review see Irwin et al. 2004), it seems that there is no strong evidence for an intra-specific communicatory function. Latrine-use is described for species of *Lepilemur* and *Hapalemur* (Irwin et al. 2004), and while lemur latrines are prominently positioned, these locations are not obvious to conspecifics as they are many metres below their normal route of travel. As individuals were never recorded investigating these sites, the authors' interpretation that lemur latrines signal intra-specific resource defence seems unlikely.

Predator avoidance

Scent-marks may be placed in concealed places to avoid detection by predators. Experiments with wild European kestrels, *Falco tinnunculus,* showed that this species can identify prey patches from the ultraviolet cues contained in vole urine and faeces (Viitala et al. 1995), and similar selective pressure may explain why lemmings, *Dicrostonyx groenlandicus*, have "indoor plumbing" in summer (Boonstra et al. 1996). Such a system may also operate in reverse, and Mech (1977) demonstrated that prey species may intercept the territorial signs of the grey wolf, *Canis lupus,* and keep to the periphery of territories. Similarly, European hedgehogs, *Erinaceus europaeus,* avoid areas scent-marked by European badgers (Ward et al. 1997). However, the suggestion that aardwolves bury their faeces in middens to avoid detection by their prey (Kruuk & Sands 1972) is rather unconvincing, as aardwolves feed almost exclusively on *Trinervitermes* termites (Bothma & Nel 1980).

Orientation / familiarisation

The hypothesis that scent-marks serve to familiarise individuals or provide a psychological reassurance to residents, "making him feel that he belongs in every quarter" (Stoddart 1980), has been suggested by a surprising variety of authors (e.g. Kleiman 1966; Seitz 1969; Mykytowycz 1970; Ralls 1971; Ewer 1973; Walther 1978; Schilling 1979). However, as Gosling (1982) realised, most conclusions of this nature result from a lack of supporting evidence for other hypotheses and are not usually based on convincing empirical support. However, it could be that as intrusions and encounters are probably more likely to occur in border regions of the territory in many - if not all - species, the concentration of scent-marks in this area might serve to provide a home-advantage by "reassuring" the resident (see Gosling 1982). Experimental evidence from European rabbits provides some support for this hypothesis, as male rabbits were dominant over others in the presence of their own scent in otherwise neutral arenas (Mykytowycz et al. 1976). Essentially this 'resident wins' rule conforms to the predictions of the scent-matching hypothesis (Gosling 1982).

Much of the information and conclusions derived for the previous studies described above relied heavily on studies of the spatial distribution of latrine sites. These are persistent and often visually conspicuous, which makes them ideal targets for the study of population densities, and a plethora of field guides include tracks and signs of this nature. However, many previous studies where selective positioning is 'demonstrated' did not adequately control for the possibility that the study species utilised its home-range non-randomly in relation to these features of importance (e.g. grey wolf, Barja et al. 2004). The generation of random control points are rarely sufficient, but rarely - if ever - are shortcomings of this nature acknowledged. The investigation of latrine function requires not only correlational analyses of latrine spatial and temporal distribution, but also detailed investigations of individual behaviour at - and responses to - latrine sites.

1.4 Behaviour at latrines

Previous studies of European badger have focused on broad patterns of latrine-use by social group and by season (Roper et al. 1986), and have generally used remote methods. For example, Delahey and colleagues (2000) describe the method of bait marking which has been successfully employed to study territoriality and latrine-use in European badgers (e.g. Kruuk 1978). Plastic coloured beads were fed to different social groups in a peanut-based bait, followed by intensive monitoring of latrine sites which allowed the correct assignation of latrines to each social group (Kruuk 1978). On the same species, Brown et al. (1993) used a spool and line technique combined with an injected fluorescein marker, which allowed monitoring immediately after injection. However, the most comprehensive study of latrine behaviour in any species was conducted by Stewart et al. (2002). In that study, European badger latrine visits were solitary and generally brief (lasting on average twenty-three seconds), and were characterised by sniffing and scent-marking. Sniffing accounted for about 40% of a badgers' activity budget within the latrine and preceded about 79% of scent-marking events, and 78% of defecations. Individual hair clippings on visiting badgers meant that sex, mating status and approximate age were known from recent captures, but the researchers found no significant differences in scent-marking relating to these factors. Although squat-marks were non-randomly distributed, being centred on paths running through the latrines, there was no obvious tendency for over-marking, and insufficient data were available to determine any differences in defecation rates between the sexes.

Motivated to understand the mechanisms of transmission of a zoonotic parasite, Page and colleagues (1999) studied the visitation patterns of other species to the latrines of racoons, *Procyon lotor*. *Baylisascaris procyonis* (roundworm) eggs have been found in the faeces and latrine sites of racoons, and these parasites have been shown to cause fatal or severe central nervous system and ocular disease in humans (Page & Swihart 1998). Their results indicate that 14 species of mammal and 15 bird species visited racoon latrine sites, some of which actively foraged within the latrine. Loguidice (2001) and Page et al. (2001) went further and studied the foraging behaviour of two species of small mammals within the latrine. Foraging strategies of the white-footed mouse, *Peromyscus leucopus,* and the Allegheny woodrat, *Neotoma magister,* determined their susceptibility to infection by *Baylisascaris*. While woodrats carried whole faeces to food caches, white-footed mice primarily extracted seeds from the faeces within the latrine. Thus woodrats were more susceptible to infection, since eggs take 2-4 weeks to embryonate. Despite this rather detailed knowledge of the use of latrines for other purposes by other species, practically nothing is known regarding patterns of behaviour by the racoons themselves. In common with the patterns of studies described by Hutchings & White (2000) for mustelids, the scent-marking behaviour of species has only generally been investigated in detail in those that act as either disease reservoirs (e.g. European badgers and racoons) or keystone species for conservation (e.g. common otters).

Irwin et al. (2004) documented the use of latrines by two wild lemuriform primates, *Lepilemur* spp. and *Hapalemur griseus*. Although the majority of primates have a reduced reliance on olfaction, lemurs and other prosimians remain reliant to some extent on olfactory communication (Epple 1986). Unfortunately, individuals were not recognisable and observations were restricted to remote monitoring, with occasional anecdotal defecation events described. During these observations it seemed that the group defecated individually, sequentially and in a characteristic order, with adults defecating first. Although the authors concede that more detailed observations are required, the evidence seems to point to resource defence for the function of latrine-use. However, as these latrines were located along the ground and resulted from arboreal defecation, I see no evidence that this is any more than parasite avoidance as Gilbert (1997) suggested for red howling monkeys, as the authors do not provide evidence that lemurs ever investigated latrine sites.

In common with Roper et al. (1993), I conclude that previous ideas about the function of latrines are oversimplified, and only a multi-faceted approach will allow a full understanding of the function of latrines. Such an approach should include an investigation into the distribution of latrines (both spatially and temporally), the behaviour of individuals at latrine sites, and the information that recipients are able to derive from latrine sites.

1.5 Thesis aims

The aim of this thesis is to investigate the function(s) of latrines by combining an assessment of their spatial and temporal distribution with a detailed analysis of individual behaviour at latrine sites, and through faecal presentation experiments.

In Chapter 2, I investigate the spatial and temporal distribution of meerkat latrines and latrine-use. I estimate home ranges and determine whether latrines are more likely to be situated in key areas of the home range and whether, on a more local scale, their distribution is related to structural features or refuges. I then go on to investigate patterns of latrine-use in relation to breeding status, season and the encounter events with neighbouring groups and extra-group individuals. In Chapter 3, I investigate the behaviour of individuals at latrine sites. Specifically, I investigate sex/dominance/age-biases in behaviour that might indicate function, and conduct an experimental presentation to test the mate-defence hypothesis for latrine-use. In Chapter 4, I describe a preliminary faecal presentation experiment, which I conducted to assess the discriminatory ability of potentially prospecting subordinate adult males, particularly with regard to kin discrimination. In Chapter 5, I summarise and discuss the general findings of the thesis, highlight any shortcomings and suggest potential future areas of research.

1.6 Study species

1.6.1 Phylogenetic and geographic distribution

The meerkat is a small (<1kg), diurnal, group-living carnivore belonging to the family Herpestidae (Veron et al. 2004). The Herpestidae includes 37 extant mongoose species from 18 genera, which are primarily distributed in Africa, and mostly solitary (Veron et al. 2004). *Suricata* is a monotypic genus, confined to southern Africa (including South Africa, Namibia, Botswana and Angola), and is locally common in the South-West Arid Zone and adjacent Southern Savanna, Karoo and Highveld regions (Skinner & Smithers 1990; Estes 1991).

1.6.2 Social organisation

Meerkats are obligate cooperative breeders, living in groups of 2-49 individuals (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 assist in rearing subsequent litters of the dominant pair (Doolan & Macdonald 1997; Clutton-Brock et al. 1998b; Clutton-Brock et al. 2001a). Meerkats exhibit high reproductive skew, with the dominant pair almost monopolising breeding (Griffin et al. 2003). Breeding success is strongly correlated with rainfall (Clutton-Brock et al. 1999a), and litters of 1-7 pups are “babysat” at a burrow until first emergence at around three weeks of age (Doolan & Macdonald 1997). Occasional mixed litters are reared with up to 13 emergent offspring from as many as five different mothers (Clutton-Brock unpublished data). Pups begin travelling with the group at four weeks of age, and are provisioned with invertebrates and small reptiles by (mainly subordinate) group members for their first three months (Brotherton et al. 2001). In contrast to banded mongoose, *Mungos mungo* (Cant 1998), there is no evidence of bonds between particular helpers and particular pups (Brotherton et al. 2001). Neither contributions to babysitting (Clutton-Brock et al. 2000), nor pup provisioning (Clutton-Brock et al. 2001a) are correlated with kinship, but rather with helper age, sex and short-term variations in foraging success. Meerkat groups defend territories against intruders which take the form of neighbouring groups, extra-group males engaging in prospecting forays, evicted females and transient or splinter groups. Territory size is about 2-5km^2 (Manser & Bell 2004) and defence is achieved by scent-marking (Gsell 2002), visual displays (Ewer 1963) and fighting (Doolan & Macdonald 1996). Individuals reach sexual maturity at around twelve months of age and disperse with same-sexed group members, at around 18-30 months of age

(Clutton-Brock et al. 1998a). Males either immigrate into an existing group by deposing and evicting the existing dominant male, or form a new group with unrelated female coalitions (Young 2003). Females never immigrate into existing groups (Clutton-Brock unpublished data). Behavioural (Doolan & Macdonald 1996) and genetic (Griffin et al. 2003) data show that breeding opportunities in subordinate female meerkats are restricted to encounters with extra-group males engaged in extra-territorial forays. Subordinate females are evicted from their philopatric group by the pregnant dominant female in the latter stages of her (the dominants') pregnancy (Clutton-Brock et al. 1998a). Eviction is correlated with subordinate age and pregnancy status, with older and pregnant females more likely to be evicted (Young 2003). In general, female dispersal is forced, but is voluntarily undertaken by males.

1.7 Study site

1.7.1 Location

The Kalahari Meerkat Project was established in 1993, and is based on the Kalahari Research Trust's Kuruman River Reserve and surrounding ranchland. This site is situated 29km west of Van Zylsrus in the southern Kalahari, in South Africa's Northern Cape (28°58'S, 21°49'E).

Figure 1.1 The location of the study site (arrow) within Southern Africa.

1.7.2 Habitat and climate

The study site was bisected by the dry bed of the Kuruman River, and consisted of sand dune, river terrace and river bed habitats (Rooyen et al. 1991). Although most of the study site was grazed primarily by reintroduced and naturally occurring native ungulates (including Gemsbok, *Oryx gazella,* Springbok, *Antidorcas marsupialis,* Blue wildebeest, *Connochaetes taurinus,* Eland, *Taurotragus eland,* Red hartebeest, *Alcelaphus buselaphus,* Steenbok, *Raphicerus campestris,* and Common duiker, *Sylicapra grimmia*), some areas were still grazed by domestic livestock, and the vegetation of the entire study site was shaped by recent overgrazing. Dunes and inter-dune slacks were sparsely spotted with Camel thorn acacia, *Acacia erioloba,* Black thorn, *Acacia mellifora* Grey camel thorn acacia, *Acacia haemotoxylon,* Shepherd’s tree, *Boscia albitrunca,* Velvet raisin bush, *Grewia flava* and Buffalo-thorn, *Ziziphus* *mucronata*, but were typified by perennial grasses (*Aristida*, *Eragrostis*, *Stipagrostis* and *Schmidtia* spp.). These grasses also occurred on the river terraces, which were dominated by shrubs including Drie doring, *Rhigozum trichotomum*, and *Monechma spp.* The riverbed was mostly non-vegetated but contained scattered *Ziziphus mucronata*, and thickets of introduced Glandular mesquite, *Prosopis glandulosa*, the latter being periodically cleared as part of a government-funded exotic species removal programme (‘Working for Water’). The riverbanks were lined with large *Acacia erioloba* trees.

The study area experiences two distinct seasons (Clutton-Brock et al. 1999a), a cold-dry season (May-September) and a hot-wet season (October-April). Mean monthly rainfall at the study site was recorded during the study period using a rain gauge and proved to be an order of magnitude greater in the hot-wet season ($\bar{x}$ = 31.6mm, range 59.3 - 0.1mm per month) than the cold-dry season ($\bar{x}$ = 3.1mm, range 0 - 12mm) (Figure 1.2). Mean annual rainfall at the study site was 250mm (Sharpe 2004). Daily maximum and minimum air temperatures were measured using an alcohol thermometer suspended in the shade (Figure 1.3). Temperatures ranged from a mean daily maximum of 36.1^{o}C and minimum of 17.0^{o}C for the hottest month (December) to a mean daily maximum of 21.7^{o}C and minimum of 1.7^{o}C for the coldest month (July).

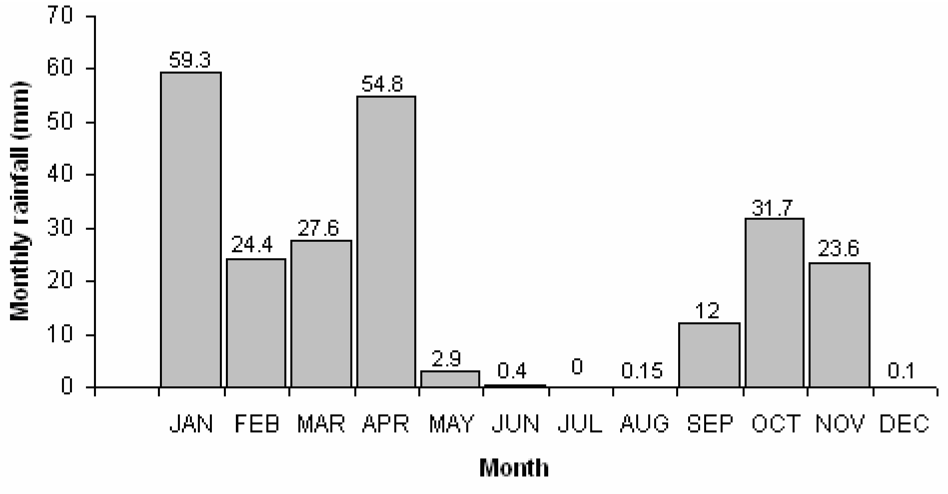


Figure 1.2 Mean monthly rainfall (mm), at the study site (May 2003 to December 2004).

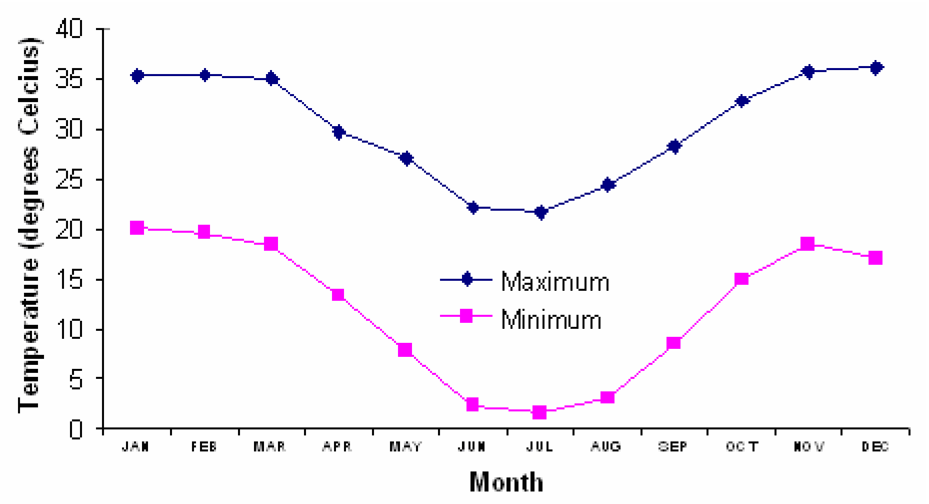


Figure 1.3 Mean daily maximum and minimum temperatures (^{o}Celsius) at the study site (May 2003 to December 2004).

1.7.3 Ecology

Meerkat groups emerge from their burrow at sunrise before setting off to forage together. During the hotter months of the year, groups retreat to a burrow, bolthole or shade until the cooler late afternoon period, but forage throughout the day in winter.

Meerkats are exposed to attack by predators when their heads are below the substrate digging for prey, and often a sentinel looks out and warns the group of impending danger (Clutton-Brock et al. 1999b; Manser 1999), and several thousand boltholes that are used for refuge are maintained throughout their home range (Manser & Bell 2004).

As meerkats forage for subterranean prey with their heads below ground, they are vulnerable to a diverse array of predators. All large terrestrial predators were eliminated from the study area during the previous century as a result of farming practices, and many aerial predators have suffered similar persecution. However, a number of meerkat predators remain at the study site and include mammalian carnivores (African wild cat, *Felis sylvestris,* Slender mongoose, *Herpestes sanguineus,* Yellow mongoose, *Cynictis pencillata,* Cape fox, *Vulpes chama),* reptiles (Rock monitor, *Varanus exanthematicus,* Cape cobra, *Naja nivea,* Puff adder, *Bitis arietans),* and birds of prey (Tawny Eagle, *Aquila rapax*, Martial Eagle, *Polemaetus bellicosus,* Black-breasted snake eagle, *Circaetus pectoralis,* Giant eagle owl, *Bubo lacteus,* Spotted eagle owl, *Bubo africanus,* Pale chanting goshawk, *Melierax canorus).* Domestic dogs, *Canis familiaris,* and cats, *Felis domesticus,* were also present.

Meerkat vocal communication has been thoroughly investigated by Manser (1998), who most notably demonstrated that meerkats employ a sophisticated system of vocalisations including referential and urgency-dependent alarm calls (Manser 2001; Manser et al. 2001, 2002). In contrast, the scent-marking behaviour of meerkats is poorly understood, and has been investigated previously on only two occasions. Moran & Sorensen (1986) showed that scent-marks were repeatedly placed at specific locations in captivity, and field-based presentation experiments (Gsell 2002) showed that individuals spent greater time investigating the faeces of dominant and pup faeces. All previous studies of scent-marking in the Herpestidae have been conducted in captivity (dwarf mongoose, Rasa 1973; Indian mongoose, Gorman 1976, 1980; Gorman et al. 1974; banded mongoose, Ianovschi 2001), and so although it is clear from these studies that mongooses are heavily dependent on olfaction, very little is known about how this affects their behaviour in the field.

1.8 Study population

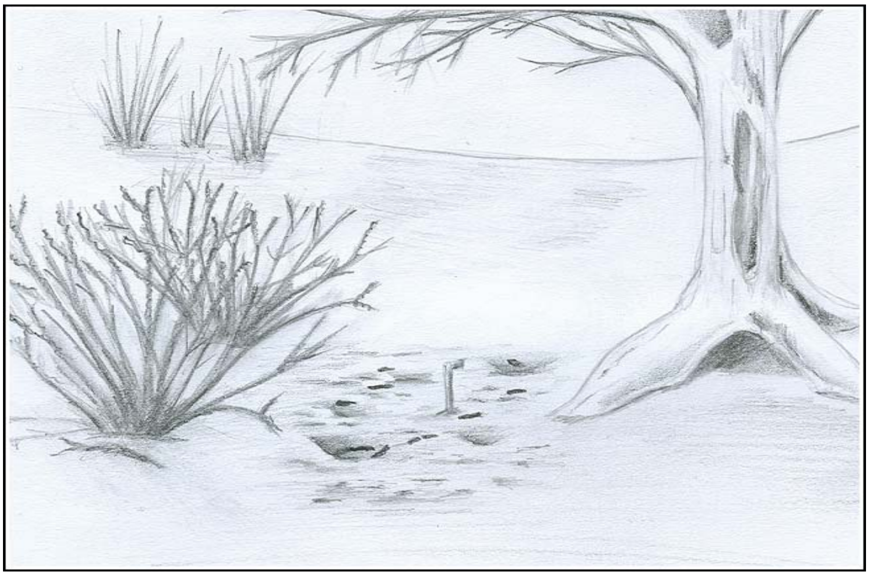
The study population has been studied since 1993 by Professor Tim Clutton-Brock's Large Animal Research Group at the University of Cambridge, United Kingdom. Thirteen groups of wild meerkats were habituated to close human observation and handling during the study, such that they could be approached to within <0.5metres while foraging. All individuals were given a small hair-dye mark on their pelage to allow rapid field identification, and one individual in each group was fitted with a radiocollar (Sirtrack®). In addition, unique transponders (Identipet®) were inserted under the skin of pups between the shoulder blades at two to three weeks of age for identification confirmation where necessary. The age of over 95% of all study individuals was accurately known (usually to the nearest day, but no more than three days out) as they had been followed since birth. Maternal identity was easily assigned by weight loss on parturition, and paternity was derived based on 12 variable micro-satellite loci, combined with the identity of the mother and the likely father (Griffin et al. 2003; Spong unpublished data). Individuals were classified depending on their age and were pups from 0-3 months, juveniles from 3-6 months, sub-adults from 6-12 months, and adults >12 months. Group composition at the mid-point of the study period is shown in Table 1.2.

Table 1.2 Group composition for the study population in January 2004 (mid-study), showing the number of each category and total group size (including pups).

Group ID	**Adult males**	**Subadult males**	**Juvenile males**	**Adult females**	**Subadult females**	**Juvenile females**	**Pups**	**Group size**
B	4	0	0	2	0	0	0	6
D	7	0	0	4	0	0	5	16
E	3	0	0	16	1	0	5	25
F	7	1	0	13	0	0	0	21
GG	2	0	0	3	0	0	4	9
L	7	1	0	2	1	0	3	14
MM	5	0	0	3	0	0	0	8
RR	8	1	0	1	1	0	0	11
V	9	1	0	6	1	0	3	20
W	7	1	0	5	0	0	4	17
Y	10	2	0	7	0	0	2	21
ZZ	4	0	0	5	5	0	0	14
						Group size ($\bar{X}$ ± SE):		15.2 ± 1.71

2

The spatial and temporal distribution of meerkat latrines reflects intruder diversity and suggests a role in mate-defence



Prepared in accordance with guidelines for submission to the journal Animal Behaviour

2.1 Abstract

Cooperative meerkats, *Suricata suricatta,* defend territories and deposit faeces and other scent-marks in specific latrine sites. The spatial and temporal distribution of these latrines maximises the chance of discovery by three main types of potential intruder. Firstly, neighbouring groups encroach onto territories from predictable directions. Each group shared at least one latrine on a long-term basis with each known neighbour, which may facilitate efficient inter-group monitoring. In contrast, prospecting males and transient groups are relatively erratic in their direction and timing of intrusions. As meerkat territory borders are relatively long, the chance of more unpredictable intruders missing widely spaced boundary scent-marks is high. Latrines occurred at significantly higher densities in core against border regions, which may be the most effective strategy to intercept these intruders. Latrine detection is further promoted by strategic local and temporal positioning. During intrusions, prospectors meander from refuge to refuge in search of groups, and latrines are significantly closer to refuge than control sites which account for non-random group movement. Although latrine-use occurred throughout the year, it was significantly more likely on days when extra-group individuals were encountered, and moderately more likely during periods when resident females were sexually receptive. In common with other species, elevated rates of latrine-use coincided with the peak-dispersal period. The spatial and temporal distribution of latrines indicates that intruders are intended recipients, and as these are generally prospecting males, an important role in mate-defence is suggested.

2.2 Introduction

Carnivores regularly deposit faeces and other scent-marks at specific locations known as latrines (for reviews see 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 represent 'scent-fences' and function by deterring intruders from entering occupied areas 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 opponents scent or a scent-mark that it was seen to deposit (Gosling 1982). Due to 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 maximising the likelihood of latrine detection. 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 such a system uneconomical, especially where territory boundaries are relatively long (Gorman 1990). Within the hyaenidae for example, Gorman & Mills (1984) provide evidence that scent-marking strategies are dependent 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, Kruuk 1972), whereas species occupying relatively large home ranges (e.g. brown hyaena, Mills et al. 1980) adopt a hinterland marking strategy, with latrines and scent-marks scattered throughout the territory. Computer-simulated intrusions demonstrate that the hinterland marking strategy observed in brown hyaena is effective in ensuring signal detection by intruders (Gorman & Mills 1984). In relatively large territories, the chance of intruders missing widely spaced boundary scent-marks selects for centrally clustered scent-marking patterns (Gorman 1990).

In addition to the general scent-marking strategy adopted by a species, the efficacy of signal transmission may be further increased by strategic positioning on a more local scale which promotes signal discovery and longevity (Alberts 1992; Bradbury & Vehrenkamp 1998). Many species primarily deposit scent-marks on or near conspicuous landmarks such as rocks, trees or crossroads (for reviews see Eisenberg & Kleiman 1972; Macdonald 1985), and/or in locations that potentially provide protection and increase signal longevity (e.g. European badger latrines under confiner trees, Kruuk 1978). Although many studies show non-random positioning of scent-marks in relation to prominent or potentially protective features, few account for the potential non-random movement of animals in relation to these features (but see Gilbert 1997). Seemingly selective positioning of scent-marks may therefore result from a more general affinity for these features.

Alongside their role in territorial demarcation and defence, it has been suggested that 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: males visit boundary latrines more often than females, and display a peak in latrine visits 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, Erlinge 1968; grey wolf, Peters & Mech 1975; North American beaver, Müller-Schwarze & Heckman 1980; water vole, Woodroffe & Lawton 1990; pine marten, *Martes martes*, Helldin & Lindstroem 1995).

This study investigates the function of latrines by examining their spatial and temporal distribution in a population of wild meerkats in the southern Kalahari. Meerkats are obligate cooperative breeders, living in territorial groups of 2-49 individuals (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 assist in rearing 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). Either sex may form new groups with coalitions of unrelated opposite-sex individuals, but males often immigrate into an existing group by deposing the resident males (Young 2003). I estimate home ranges and territories and determine whether latrines are more likely to be situated in particular areas, and whether their local distribution is related to specific structural features and refuges that may promote signal discovery or longevity. I then examine temporal patterns of latrine-use in relation to season, the breeding status of resident females, and encounter events with neighbouring groups and extra-group individuals. If meerkat latrines function in mate-defence, their spatial and temporal distribution should maximise the likelihood of intercepting intruding rivals.

2.3 Methods

2.3.1 Study site and population

I undertook this study between May 2003 and December 2004 on recovering ‘ranchland’ in the southern Kalahari, 29km West of Van Zylsrus in South Africa’s Northern Cape (28°58’S, 21°49’E). Further details of the study site are given in Clutton-Brock et al. (1999c). I collected data from twelve groups of wild meerkats, habituated to close human observation and handling, with each group visited at least once every three days for at least three hours. All individual meerkats were given a small hair-dye mark on their pelage to allow rapid field identification, and one individual in each group was fitted with a radiocollar (Sirtrack®).

2.3.2 Latrine description and classification

Latrine sites contain concentrated accumulations of faeces and are often associated with the deposition of other scent-marks. Latrines contained at least two faeces within one metre of each other, but typically 5-100+ faeces occurred in a 0.5- 6m^2 area. This area was covered with multiple small pits (about 30mm 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. Latrines were assigned to one of three categories based on observed patterns of use during the study: ‘single-use latrines’ were visited by a single group only once; ‘multiple-use 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. Individual meerkats generally defecated between one and three times per day, either at a latrine site or in isolation (i.e. away from a latrine).

2.3.3 Spatial data collection

Location data were recorded using handheld eTrex (Garmin®) Global Positioning System (GPS) units and transferred into the GIS software program ArcView© GIS 3.3 (Environmental Systems Research Institute, Redlands, California). Coordinates of group location were recorded every fifteen minutes, and additional coordinates were taken whenever groups visited latrines. In order to maximise independence between samples, a single randomly selected coordinate was extracted from each observation session, and home ranges and territories were estimated from these locations using the Animal Movement extension in ArcView®. To estimate home ranges I employed the 95% fixed kernel method (Worton 1989), and 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 202.9 ± 10.5 ($\bar{X} \pm$ SE) coordinates per group (range: 160-260), which vastly exceeds the minimum of 50 suggested by Seaman et al. (1999). Home ranges were further divided into core and border areas. To distinguish between border and core areas, I calculated the percentage of each home range that overlapped with each overlapping neighbour. At the 95% kernel, there were 15 dyadic overlapping regions. The area of each of these overlaps was individually divided by 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 territory boundary. This approach allowed overlapping border regions to be estimated for groups with neighbouring non-study groups, whose home ranges could not be estimated.

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 latrine site and isolated faeces. All measurements >3m were taken at crouching height using a handheld rangefinder (Motorola® DME Laser 3000A) to the nearest 10cm, and measurements <3m were taken with a tape measure to the nearest 1cm. The distance to refuge was measured to the overhang of the hole. Seven species of tree occurred at the study site and were included in the analysis: Camel thorn acacia, *Acacia erioloba,* Black thorn, *Acacia mellifora,* Grey camel thorn acacia, *Acacia haemotoxylon,* Shepherd's tree, *Boscia albitrunca,* Velvet raisin bush, *Grewia flava* and Buffalo-thorn, *Ziziphus mucronata,* and the invasive Glandular mesquite, *Prosopis glandulosa*. Further data on vegetation can be found in Russell et al. (2002). Sample-specific measurements and controls are described below.

Latrine site surveys

All multiple-use latrine sites (n=150) were located retrospectively 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 minutes after latrine-use ($\overline{x} \pm SE = 13.05 \pm 1.06$). This controlled for the possibility that meerkats foraged non-randomly in relation to the features of interest. Distances were measured from the centre of each latrine and its control site.

The distance to the closest breeding and non-breeding burrow were measured from each multi-use latrine site. A 'breeding' burrow was used to "babysit" pups for four or more consecutive days during the study period, and a ‘non-breeding burrow’ was any other burrows used for at least one night. This definition removed the likelihood of assigning greater significance to non-breeding burrows, as pups are typically moved to boltholes and minor burrows following 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-minutes. Those latrines where no control point was collected within 14 days were excluded.

Individual faeces surveys

Meerkats deposited faeces within latrine sites or in isolation (i.e. not in latrine sites), and data were collected from observed events of both types. As the position of multiple faeces was recorded during each latrine visit, a single randomly chosen sample was analysed from each visit to avoid pseudoreplication. In addition to the standard measurements described above, whether > 50% of the individual faeces was in a pit and/or beneath the canopy of vegetation (including trees, shrubs or grass clumps) was recorded. Corresponding control measurements were taken from the location of the depositing individuals’ tail-base ten-minutes post-defecation. The tail-base was chosen as a control point as it is a small (ca.12mm width) 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 minutes post-defecation).

2.3.4 Temporal data collection

The occurrence of all observed latrine visits were recorded and examined in relation to temporal and social factors. Observation periods were classified by (a) season, (b) the occurrence of inter-group encounters and (c) whether any resident females were in oestrous. Only observation periods lasting for one hour or more were used in the analyses, as latrine-use was less likely to coincide with brief visits than were inter-group encounters or the determination of oestrous state.

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 I refer to these months as the ‘breeding’ period. The cooler and drier months between May and September result in vastly reduced reproductive activity, and I refer to these months as the ‘non-breeding’ period. The number of latrine visits per full observation session was calculated for each group during breeding and non-breeding periods. Expected values were determined by assuming that rates of latrine-use (per observation effort) remained constant throughout the year. Encounters with other groups and extra-group individuals were recorded *ad libitum*. Inter-group encounters typically involved a stereotyped threat display or ‘war dance’ with one group usually retreating prior to physical fighting. Prospecting males commonly approached the edge of the group, and were often persistently chased off by residents. Although behavioural signs of oestrous are rare and often restricted to the mate-defence activities of dominant males, it was possible to determine 51 days of ‘observed’ oestrous during the study period. As parturition dates can be accurately determined from dramatic weight loss, and females typically enter oestrous periods between four and 12 days post-partum, additional periods of ‘derived’ oestrous were estimated for the study period, and covered a further 476 days of observation. The rate of latrine-use for non-oestrous days was compared separately with ‘observed’ and ‘derived’ periods of oestrous.

2.3.5 Analysis

All statistical tests were carried out in Minitab$^{\circledR}$ release 12.21. I used parametric statistical tests unless the data differed significantly from normal (based on the Anderson-Darling test for normality). In these cases, equivalent non-parametric statistics were used.

2.4 Results

Each group visited 6-24 multi-use latrines ($\bar{x} \pm$ SE = 12.5 ± 6.17), and 17-37 single-use latrines ($\bar{x} \pm$ SE = 24.7 ± 2.15) during the study period. 17 shared latrine sites were visited, and each group with overlapping home ranges shared at least one latrine with each neighbour (except one group whose home range shifted dramatically during the study period).

2.4.1 Spatial distribution

Mean home range was 2.06 ± 0.72 km^2 ($\bar{x} \pm$ SE) (range: 0.91-3.30, $N = 12$) with a mean perimeter length (length of the 95% adaptive kernel) of 8.88 ± 0.40 km ($\bar{x} \pm$ SE) (range: 6.52-11.18, $N = 12$) (Figure 1.1). Exclusive ‘territory’ areas, as estimated by the 85% kernel, had a mean area of 1.08 ± 0.18 km^2 ($\bar{x} \pm$ SE) (range: 0.31-2.48, N

= 12) and had a mean perimeter length of 6.08 ± 0.38 km ($\bar{X}$ ± SE) (range: 3.13 – 7.93, *N* = 12) for the exclusive area (85% kernel).

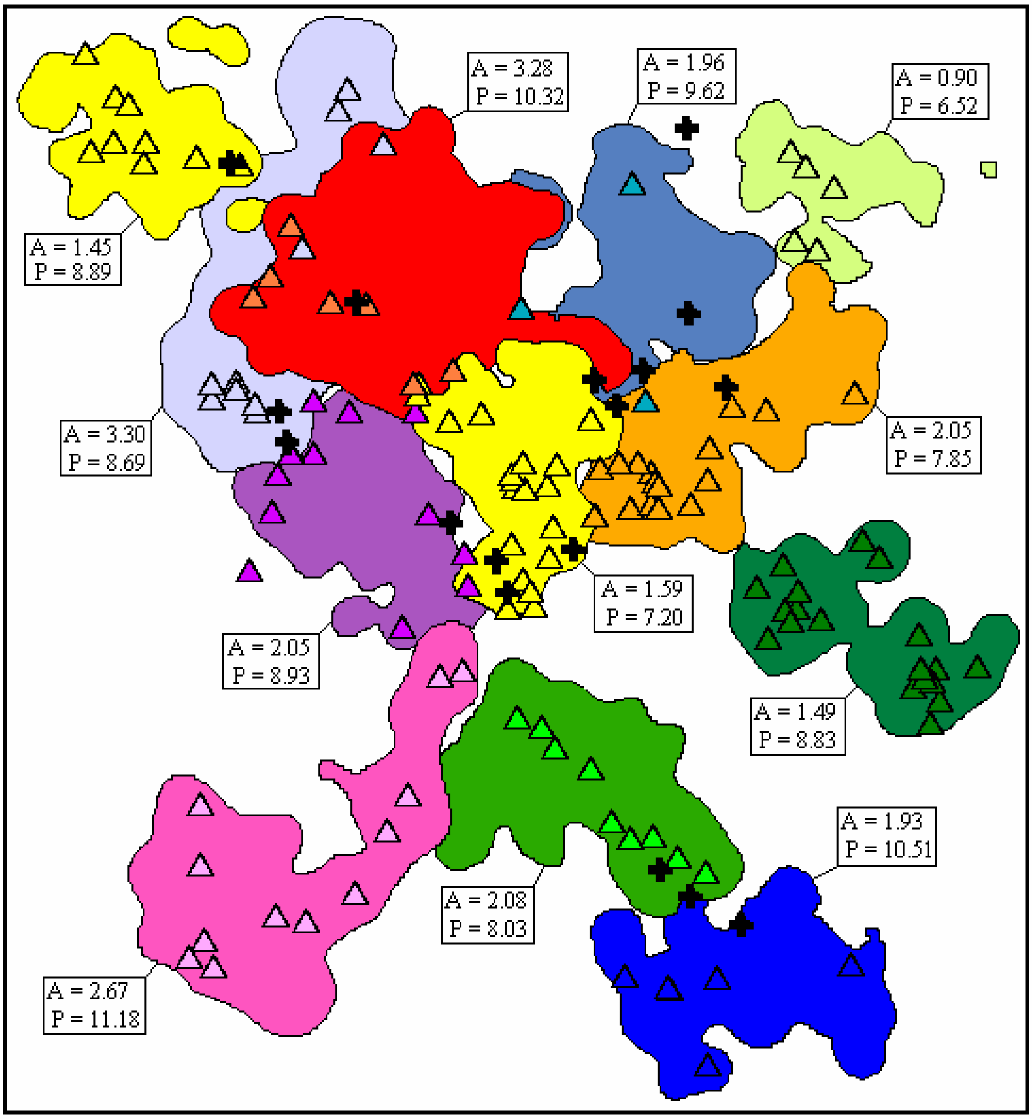


Figure 2.1. Home ranges for the study population showing all multi-use (Δ), and shared (✚) latrines. Home range areas (A) in km^2, and perimeter length (P) in km, are shown for each group.

Each group shared a mean overlapping home range area with each habituated neighbouring group of 0.22 ± 0.096 km^2 (range: 0.023-1.43, *N* = 14 overlapping areas) (Figure 2.2).

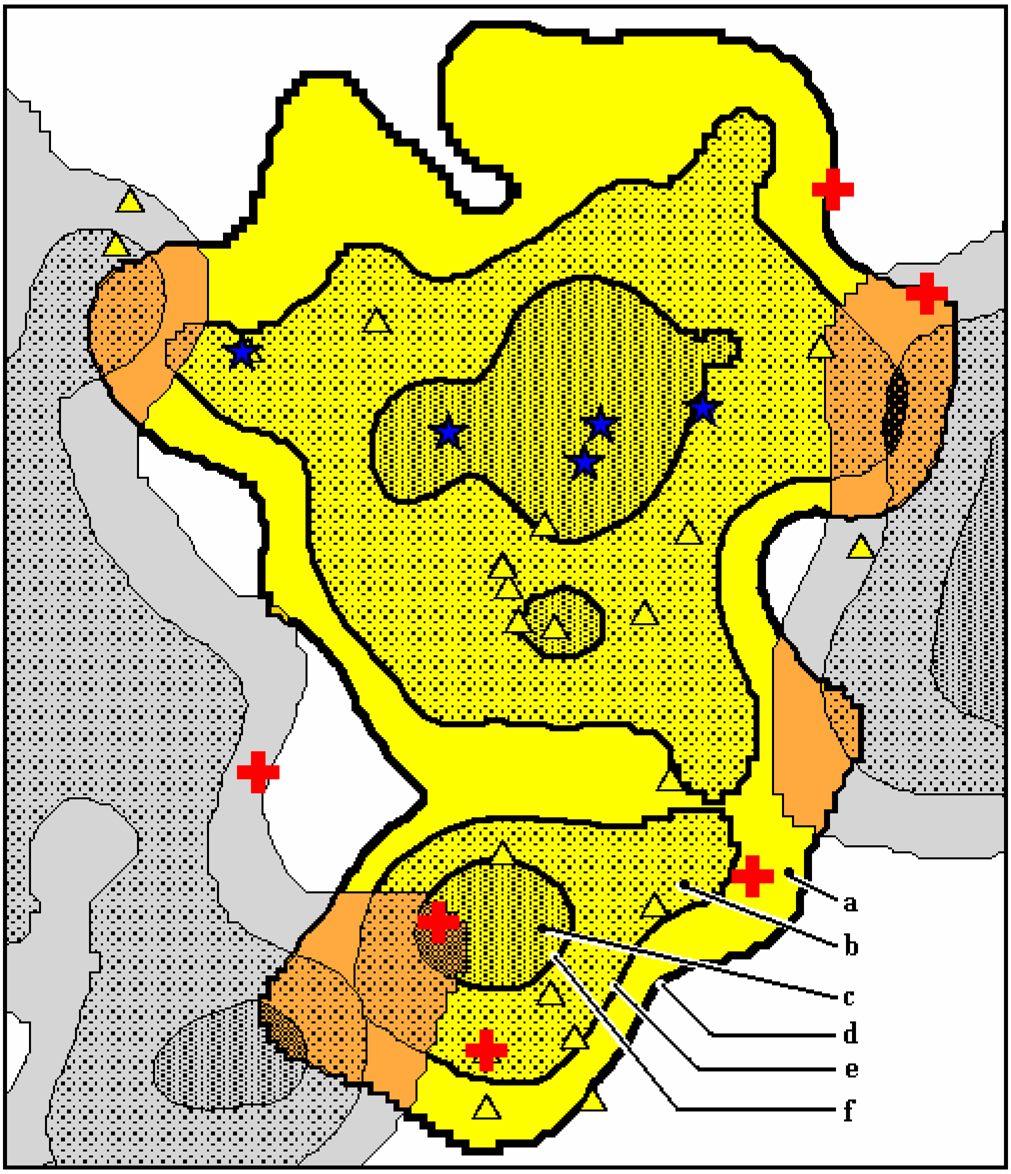


Figure 2.2. A sample home range for one group (surrounded by bold line) showing (a) home range area, (b) territory border area, (c) territory core area. Areas are divided by (d) 95%, (e) 85% and (f) 65% kernels. Home ranges for two neighbouring groups are plotted on either side, and overlapping areas are shown. Stars are breeding burrows, crosses are shared latrines and triangles are multiple-use latrines.

Multiple-use latrines occurred at significantly higher density in core compared to border areas of the home range (Wilcoxon signed-ranks test: $T = 6$, $N = 12$, $P = 0.009$). When the border density was artificially increased by including multiple-use latrines that occurred outside of the home range, this remained highly significant (T = 8, N = 12, P = 0.017). Within the 85% exclusive kernel (i.e. the territory) multiple-use latrines occurred at significantly higher density in core (65% kernel) compared to border (between 85% and 65% kernels) areas (T = 9, N = 12, P = 0.021). Similarly, single-use latrines occurred at higher densities in the territory core (T = 3, N = 12, P = 0.005).

Latrines were ($\bar{X}$ ± SE) 360.6 ± 26.8 metres, N = 125, from the closest breeding burrow (compared to 352.2 ± 26.0 metres for their control sites), and 160.5 ± 12.4 metres from the closest non-breeding burrow (compared to 158.56 ± 9.26 metres for controls). Furthermore, latrines were no closer to either breeding or non-breeding burrows than control sites (Wilcoxon signed-ranks test: *Breeding burrows*, T = 3842, N = 125, P = 0.94; *Non-breeding burrows*, T = 3775.5, N = 125, P = 0.81).

Latrines and individual faeces deposited in latrines were significantly closer to a refuge than their appropriate controls (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). Individual faeces deposited in isolation (not in latrines) were also significantly closer to a refuge than their control sites (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 (*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; *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 (Chi-square test: X^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 ($X^2_1 = 0.29$, $P = 0.59$). There is no significant difference between latrines and control sites in association with dead trees ($X^2_1 = 1.77$, $P > 0.10$), grass ($X^2_1 = 1.96$, $P > 0.10$) or shrubs ($X^2_1 = 0.47$, $P > 0.30$) but control sites were more likely to have forbes <2m than were latrines ($X^2_1 = 4.26$, $P < 0.05$). Latrines were significantly more likely to have pits <2m than were their control sites ($X^2_1 = 58.17$, $P < 0.001$).

2.4.2 Temporal distribution

Latrine-use occurred at greater rates in the non-breeding period (May to September) than in the breeding period (October to April) (Chi-square test: $X^2_1 = 26.09$, $P < 0.001$) and was significantly more likely to occur on days when groups encountered extra-group individuals than on days when no encounter occurred ($X^2_1=41.91$, $P < 0.001$) (Figure 2.3). The rate of latrine-use was significantly associated with rates of encounter with extra-group prospecting males (Pearson's correlation: $r = 0.795$, $N = 19$, $P < 0.001$). Unfortunately only four extra-group encounters occurred that did not result in temporary prospecting, and so the effects of extra-group encounters alone could not be determined.

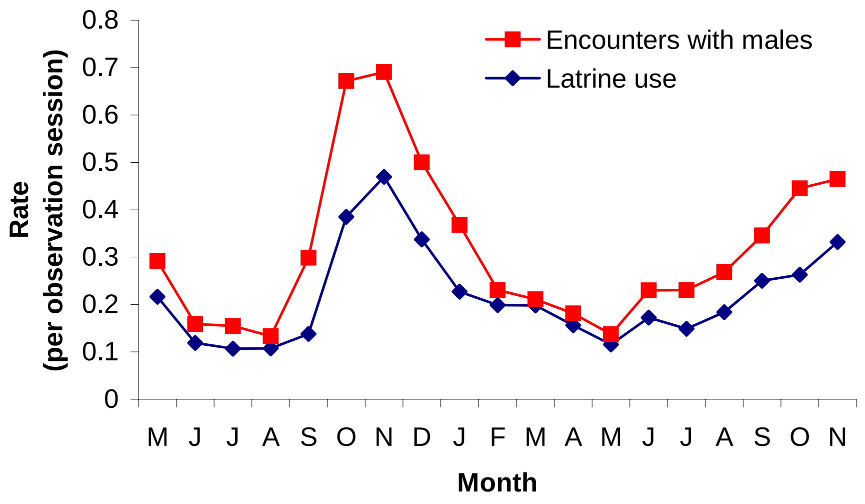


Figure 2.3. Rate of latrine-use and encounters with extra-group males through the study period (N=13 groups).

Compared to non-oestrous days, latrines were no more likely to occur on days of either 'observed' or 'derived' oestrous for a resident female (Chi-square test: *Observed oestrous*, $X^2_1 = 1.08$, $P = 0.30$; *Derived oestrous*, $X^2_1 = 0.88$, $P = 0.35$). Although the rate of latrine-use was correlated with the number of conceptions each month, this correlation was only marginally significant (Pearson's correlation: $r = 0.441$, $N = 19$, $P = 0.059$) (Figure 2.4).

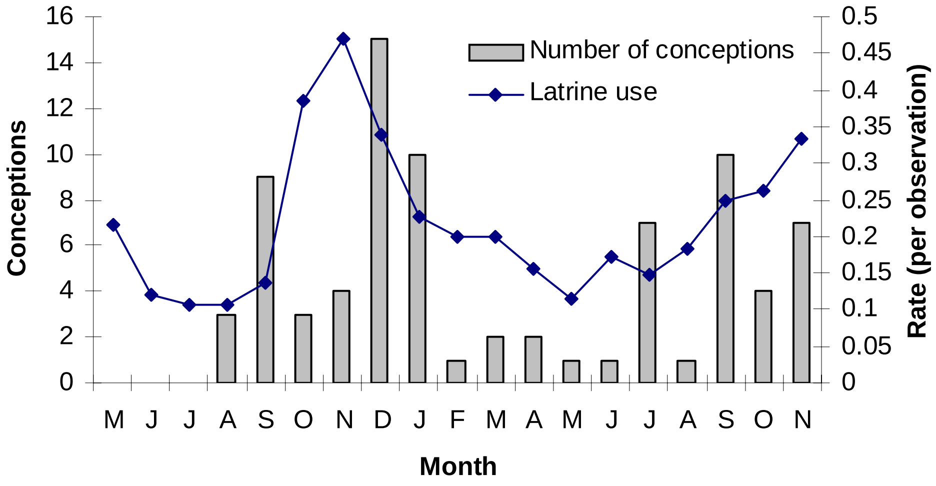


Figure 2.4. Rate of latrine-use and number of conceptions through the study period (n=13 groups).

2.5 Discussion

Meerkat latrines were distributed non-randomly both spatially and temporally, and patterns were consistent with the hypothesis that latrines serve to maximize the likelihood of intercepting intruders. Territorial residents may encounter three broad types of intruder, and the overall scent-marking strategy adopted reflected the different selective pressures resulting from this diversity in intruder type (e.g. Northern harriers, *Circus cyaneus,* Temeles 1989a, b). While a neighbouring group threatens permanent loss of space (Gosling 1987), they represent a relatively known force and encroach from predictable directions. Meerkats shared at least (and usually) one latrine site with each neighbouring group, which presumably facilitated efficient inter-group monitoring. In contrast, transient groups (dispersing groups of opposite-sex coalitions that meet and attempt to settle permanently outside their natal territories) threaten a severe loss of space, potentially taking over the entire territory, and are relatively unpredictable in their time and direction of entry. Similarly unpredictable, prospecting males threaten the dominant male with permanent takeover or loss of paternity. In response to these unpredictable intruder types, meerkats concentrated their latrines into the core regions of their territories. This maximises the likelihood of detection, as meerkat territories are probably too large to maintain an effectively marked border, and latrine local positioning further increases the likelihood of discovery.

Inter-group spacing is important, as visual encounters with neighbouring groups and/or extra-group individuals usually result in costly chases, ritualised displays or physical fights (Young 2003). Territorial incursions by neighbouring groups occur from predictable directions, and given information gained from previous encounters neighbours represent a fairly familiar quantity. Unnecessarily prolonged territorial border disputes would be deleterious, and as such are often settled by convention (Parker 1974). For example, the outcome of meerkat inter-group encounters depends primarily on relative group size, with smaller groups significantly more likely to retreat (Young 2003). Meerkat groups shared at least one latrine site with each neighbouring group and these sites are likely to facilitate inter-group information transfer and allow economical monitoring of land tenure in the surrounding territories. Some territorial carnivores respond quickly to changes in the movement patterns or disappearance of neighbours by expanding their own range (Sargeant 1972; Macdonald 1977; Kruuk & Macdonald 1985), and similarly meerkats may monitor shared latrine sites and thus reduce the cost of territorial disputes and respond to the movement of neighbouring groups by increasing their own territory. Shared latrine sites may therefore be the most economical solution to a predictable threat.

Carnivores living in high-density populations concentrate their scent-marks on or close to territorial borders (e.g. European badgers, Kruuk 1978; Pigozzi 1990; Brown 1993; Roper et al. 1993), which is generally interpreted as evidence of their role in territory defence as scent-marking along the territorial border occurs where competition is most intense. However, in relatively large territories, the chance of intruders missing widely spaced boundary marks selects for centrally clustered scent-marking patterns (Gorman 1990), and a border-marking strategy may only be economically feasible in high-density populations due to the complimentary effects of decreasing border length and an increase in the number of individuals contributing to its maintenance (Macdonald 1985; Gorman 1990). In contrast to neighbouring groups, extra-group prospecting males and transient groups may enter the territory from any direction, and may cross multiple territories during forays (Young 2003). As these home ranges have an average border length of 8.9 km, and groups travel together and so must maintain their latrines as a single group, it is not economically feasible to maintain an effectively marked perimeter. Although differences in size and ecology mean that direct comparisons across taxonomic groups must be made with caution, data from the hyaenidae show that in populations where individual patrolling units would have to travel greater than 7.5 km to mark the entire border, scent-marks are instead distributed throughout the home range (see Gorman & Mills 1984). The spatial distribution of meerkat latrines fits this general pattern, as latrines occurred at significantly higher densities in the core than the border regions of home ranges. That meerkats did not adopt a border marking strategy therefore probably reflects economic constraints, which may be particularly acute in their desert habitat. Unfortunately, variation in territory size within the study population was not sufficient to investigate intra-population variation in scent-marking strategy, but it would be interesting to see what patterns of scent-marking are adopted by herpestids inhabiting territories with relatively short borders.

Strategic positioning of meerkat latrines and faeces also occurred on a more local level, and may assist in increasing signal persistence and maximising the chance of signal discovery. In common with many other species (for review see Macdonald 1985), latrines were distributed such that the probability of their discovery by a conspecific appears to be maximised. This is unsurprising, as successive increases in signal strength result in successively smaller increments in perceived intensity (Mozell 1972), so that individuals seeking to minimize the energetic costs of scent-marking should employ strategies to increase signal 'detectibility' other than those that require significant increases in amount of material released (Alberts 1992). Meerkat latrines and faeces deposited in isolation were significantly closer to refuge than were their control sites. Although meerkat groups are always close to refuges (Manser & Bell 2004), this result is not explained by non-random movement in relation to refuge as (unlike most previous studies) stringent controls have taken this possibility into account. Neither can this be explained by a tendency to deposit latrines close to sleeping or breeding burrows, as latrines were no closer to burrows than control sites. By placing latrines close to boltholes, meerkats may increase the likelihood of discovery by intruders, as prospecting males follow a meandering course and spend long periods inspecting burrow systems (Doolan & Macdonald 1996). Prospecting individuals and transient groups are likely to encounter latrines positioned close to refuge, but whether intruders 'know' the location of latrines or find them as a result of their proximity to boltholes is not yet known. An alternative interpretation is that latrine-use is a distracting and hazardous activity and is therefore optimally performed in proximity to refuge. However, this is unlikely given that individuals spend a quarter of their total ‘within -latrine’ time vigilant (see Chapter 3) and are able to maintain vigilance during defecation.

Signal efficacy may be further increased by selectively positioning latrines such that faeces are protected and signal longevity promoted. Although latrine sites and control sites were equally likely to contain shrubs, individual faeces that were deposited in latrines were more likely to be below the canopy of vegetation than their control points, whereas faeces deposited in isolation were no more likely to be. By placing faeces below the canopy of vegetation, meerkats may increase scent-mark longevity by sheltering them from the evaporative effects of the sun and/or protecting them from occasional rain. Although many species primarily deposit scent-marks on or near obvious landmarks such as rocks, trees or crossroads (e.g. Barja et al. 2004; or for reviews see Eisenberg & Kleiman 1972; Macdonald 1985), the tendency for meerkat faeces to be placed below the canopy did not result from non-random positioning in proximity to trees, as latrines were no closer to trees than were their control sites. The placement of faeces below the canopy may instead result from the tendency of meerkats to defecate in pits produced by foraging, and a bias in favour of foraging at the base of vegetation (personal observation). By placing faeces below the canopy, indirect protection from the wind may be provided in the form of the stabilising effect of roots on the surrounding sand. Although latrines were significantly more likely to contain pits than were control sites, faeces deposited both in isolation and in latrines were significantly more likely to be placed in pits. In common with previous authors, I do not explicitly test whether the non-random positioning I demonstrate increases signal longevity, but it seems reasonable to suggest that faeces deposited under the canopy of trees, close to vegetation and in pits will have greater longevity than those exposed on the surface.

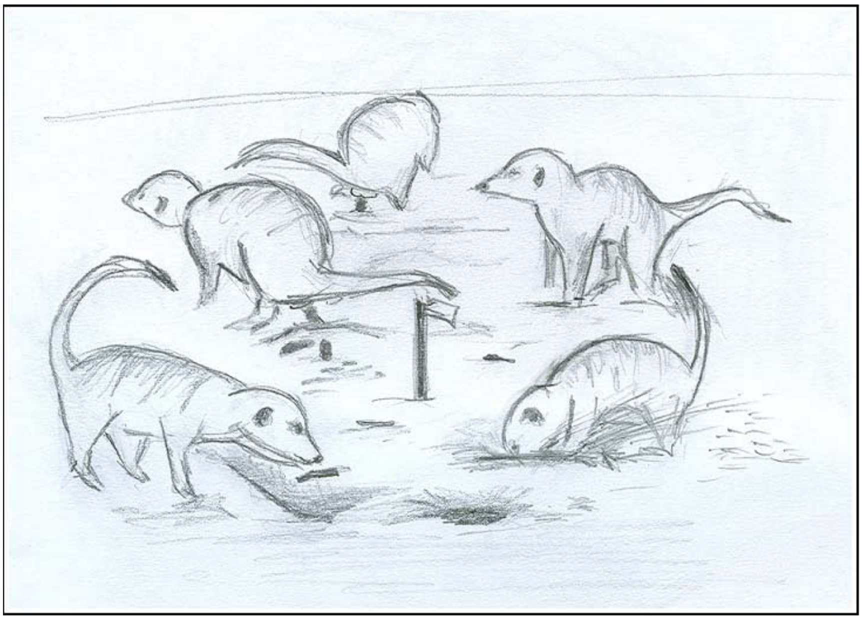
Meerkats visited latrines throughout the year, but rates of latrine-use were highest in the period of reduced breeding from May to September. This contrasts with other species where observations made throughout the year show that scent-marking increases to a peak during the mating season (e.g. common otter, Erlinge 1968; grey wolf, Peters & Mech 1975; pine marten, Helldin & Lindstroem 1995). Latrine-use has been most intensively studied in European badgers, and generally shows a seasonal peak in early spring, coinciding with the mating season (Neal 1977; Kruuk 1978; Roper et al. 1986; Buesching & Macdonald 2004). Roper and colleagues (1986) suggested that such seasonal patterns of latrine-use indicate a role of latrines in mate-defence, but I found no correlation between meerkat latrine-use and periods of sexual receptivity in resident adult females. However, the accurate determination of oestrous in meerkats is problematic, and the protocol may have resulted in the erroneous inclusion of non-oestrous days in the oestrous sample, while actual post-partum oestrous days were missed and included in our non-oestrous sample following unnoticed abortion events. Furthermore, one must be cautious in interpreting these data as indicative that latrines are not implicated in mate-defence. Meerkat groups were significantly more likely to visit latrines on days when they encountered extra-group individuals, and monthly rates of inter-group encounters 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 prospectors after the group had retreated. Given that latrines were more likely to be located in territorial core areas (where inter-group encounters rarely occur), this cannot be explained by interactions occurring in areas where latrines were more common.

If meerkat latrines serve to advertise the commitment of resident males to defend resident females (as Roper et al. 1986 suggest for the European badger), then rather than being highest in the breeding season, latrine-use may be greatest during the time of year and during social situations where the threat of take-over is greatest. As meerkats do not have a strict breeding season, prospecting males may therefore potentially reduce the reproductive success of dominant males at any time, although this is more likely at particular times of year (Young 2003). The fact that latrine-use increased in response to prospector pressure provides strong support for the mate-defence hypothesis. In species where bonds between mates last throughout the year, mate-defence may not peak during periods of female receptivity, but instead may be intensified in periods when competition for the breeding position is most pronounced. In cooperative breeding meerkats, high reproductive skew results from the reproductive monopoly controlled by the dominant pair, and although extra-group prospecting males represent a threat to paternity, they account for only 3.4% of the paternity of a dominant female's pups (Spong unpublished data). The main threat that prospecting males present to dominant males is one of dominance takeover, which primarily occurs from July to October (Young 2003). All twelve observed events of dominance take-over by extra-group males occurred in the period of reduced breeding (Young unpublished data), and the dominant position was always held by one of the usurpers for the following breeding season. By concentrating the defence of the dominant position within the period of most intense competition, males could ensure the greater proportion of reproductive success throughout the subsequent breeding year.

Further support for this hypothesis comes from the scent-marking patterns observed in another cooperative breeding carnivore, the Ethiopian wolf. Scent-marking activity reaches a peak in May and June, while the mating season runs from July to September and does not result in increased scent-marking activity (Sillero-Zubiri & Macdonald 1998). Importantly, emigration primarily occurs two to three months prior to the mating season (Sillero-Zubiri et al. 1996), which coincides with the peak in scent-marking. In cooperative breeding species, latrines may advertise the commitment and ability of resident males to defend resident females, and peaks in latrine-use coinciding with threats of take-over may reflect their mate-defence function. Both experiments and a more complete analysis of behavioural patterns at such sites are required to further substantiate this hypothesis.

3

Sex-biased scent-marking at meerkat latrines: cooperative territory defence or selfish advertisement?



Prepared in accordance with guidelines for submission to the journal Animal Behaviour

3.1 Abstract

Meerkats, *Suricata suricatta*, engage in cooperative territorial defence, including olfactory demarcation with latrines. However, the potential fitness costs and benefits of deterring intruders vary according to the sex and breeding status of residents. Reproduction is almost restricted to the dominant pair, and mature offspring assist them to raise further litters. Subordinate males gain extra-group paternity during temporary prospecting forays to other groups, and groups visit latrines in response to these encounters. Although all individuals visited latrines for similar durations, latrine scent-mark composition was highly male-biased and did not reflect group composition. This resulted from sex-biased scent-marking, as males of all categories scent-marked at significantly higher rates than females. Ultimate explanations for latrine-use appear to differ according to individual costs and benefits. For males, a mate-defence function is supported, as males preferentially over-marked female faeces, and sometimes manipulated experimental latrines to produce male-biased sites. In contrast, females may gain direct benefits by breeding with extra-group males, and so have little motivation to deter prospectors. Females scent-marked at lower rates than males but invested heavily in scent-mark investigation, spending significantly longer sniffing female scent-marks. This suggests that monitoring of reproductive status within the group is an important function of latrine visits for females. Rather than cooperatively contributing to territorial defence, individuals participate selfishly in latrine-use.

3.2 Introduction

Many social carnivores defend territories against neighbouring groups and intruding individuals, and the role of latrines in territory defence is widely accepted (Macdonald 1980). Although traditional explanations suggest that territory owners defend the minimum area to supply them with food (for a review see Davies 1980), carnivore territory size is often not correlated with group size (Macdonald 1983). This raises the question as to whether territoriality in these species is related to the defence of resources other than food. As ultimate explanations for territoriality may differ between the sexes (e.g. African lion, Packer et al. 1990; Grinnell et al. 1995; Heinsohn & Packer 1995; spotted hyaena, Boydston et al. 2001), latrines may also serve separate functions depending on the specific selective forces acting on each individual within a society. In cooperative societies, high reproductive skew means that these forces not only reflect differential selection on the sexes, but also vary according to access to reproductive partners.

Cooperative breeding meerkats live in groups of up to 49 individuals. The dominant pair almost monopolise breeding, and offspring remain in the natal group beyond sexual maturity and assist in raising further litters (Doolan & Macdonald 1997; Clutton-Brock et al. 1998b; Clutton-Brock et al. 2001a; Griffin et al. 2003). While subordinate philopatric males never sire offspring in their own group (Griffin et al. 2003), they do engage in extra-territorial prospecting forays from about one year of age (Doolan & Macdonald 1996; Young 2003). Males gain extra-group paternity during these forays (Griffin et al. 2003), and may successfully immigrate into groups by displacing the existing dominant male (Young 2003). Dominant females behaviourally suppress the reproduction of subordinate females by expelling them from the group in the latter stages of (the dominant's) pregnancy and by committing infanticide (Clutton-Brock et al. 1998b, 2001b; O'Riain et al. 2000; Young 2003). Subordinate females may occasionally breed in their own group, and may inherit the alpha rank either upon the death of the established dominant, or by forming a transient group with prospecting males encountered during eviction (Young 2003).

In common with other forms of territorial defence (e.g. Pusey & Packer 1997; Boydston et al. 2001), latrine behaviour should approximate the optimal behaviour for individual participants, which may gain differentially by sending different signals to intruding males. Due to high levels of reproductive skew for both sexes in meerkat society, the costs and benefits of deterring, tolerating or even encouraging extra-group males differ dramatically for different classes of individual. In meerkats access to mates is a more critical resource for males than females (Trivers 1972; Clutton-Brock 1988), and male-biased latrine-use would be consistent with the hypothesis that latrines are important in mate-defence, since females should not repel potential mates. The hypothesis that latrines advertise a 'commitment' on the part of resident males to defend resident females, was first suggested by Roper et al. (1986) and is based on sexual and seasonal differences in latrine-use by European badgers (Neal 1977; Kruuk 1978; Roper et al. 1986, 1993; Brown et al. 1992). The spatial and temporal distribution of meerkat latrines is superficially consistent with this hypothesis, as latrine-use is significantly more likely on days when extra-group males are encountered and during the season when dominance take-overs are most frequent (Chapter 2). However, inferences regarding latrine function based on distribution alone are weak, as scent-marks deposited by different individuals in the same location at the time may have different effects on recipients. Detailed analyses of individual behaviour at latrine sites are required before the function of latrines can be determined.

Prospecting males spend considerable amounts of time investigating latrine sites during prospecting forays (personal observations). These forays are costly and hazardous, and males would benefit by extracting information from latrine sites prior to an approach. As prospectors receive fewer chases, get closer to females and are significantly more likely to take-over groups with a low resident male to prospecting male ratio (Young 2003), group composition can significantly affect the reproductive success of prospecting males. It would therefore be adaptive for prospectors to assess group composition before committing to approaches, as this would allow a better cost/benefit assessment prior to cost incursion.

In summary, if prospecting males were able to assess group composition from latrine composition and base subsequent decisions on this information - as suggested by the work of Brown (1993) on the European badger and preliminary experiments on olfactory discrimination in meerkats (Gsell 2002) - resident males might deter prospectors by producing male-biased latrines. In contrast, subordinate females might increase their own fitness by encouraging extra-group male approaches through the production of female-biased latrines.

I combine detailed behavioural observations and an experimental test to determine whether individuals behave selfishly at latrine sites. Specifically I assess whether latrine composition reflects group composition such that demographic information might be obtained during latrine visits, and investigated the factors affecting investigation and over-marking patterns at naturally-occurring latrine sites.

Particularly I was interested in whether individuals were more likely to over-mark existing scent-marks made by members of the same- or opposite- sex. Finally, I conducted experimental presentations using latrines of controlled composition to assess whether individuals biased the composition of these sites through selective (e.g. sex-specific) over-marking.

3.3 Methods

3.3.1 Study area and population

I undertook this study between June and December 2004 on recovering ranchland in the southern Kalahari, 29km West of Van Zylsrus in South Africa’s Northern Cape (28°58’S, 21°49’E). Further details of the study site are given in Clutton-Brock et al. (1999c) and vegetation and rainfall data can be found in Russell et al. (2002). I collected data from eleven groups of wild meerkats, habituated to close human observation and handling. All individuals were given a small hair-dye mark on their pelage to allow rapid field identification, and one individual in each group was fitted with a radiocollar (Sirtrack®). The age of all study individuals was accurately known (usually to the nearest day, but no more than three days out). I recognised four age categories of individual: pups (0-3 months); juveniles (3-6 months); sub-adults (6-9 months) and adults (> 1 year).

3.3.2 General data collection and definitions

Video recordings were made of each observed latrine visit using either a Sony© CCD-TRV46E analogue or DCR-PC120E digital camcorder from a Starfoto© tripod set

52cm above ground level. Recordings were transferred to DVD via a 1394 fire-wire cable, with analogue recordings initially transferred to digital format via an A/V cable. DVD's were viewed for analysis using Microsoft$^©$ Windows Media Player (XP version) on a 15-inch monitor. The camera's field of view was set to incorporate the entire latrine site (typically covering about 8m^2), and the total time that individuals were in the latrine was recorded as the time spent within the field of view.

All individuals were followed using focal-animal sampling from the video recordings (Altmann 1974). When individuals disappeared into a refuge (a bolthole or sleeping burrow), the time that they were unseen was not included in their 'in-latrine' time. The proportion of time that individuals were engaged in: (a) scent-mark investigation; (b) vigilance, or (c) scent-marking was calculated. Individuals were considered vigilant when they were bipedal, or quadrupedal and immobile with the head raised above ground and not engaged in any other activity. I recorded four types of scent-marking in this study: (i) anal marking; (ii) chew marking; (iii) faecal marking and (iv) urine marking. Anal marking was achieved by wiping the anal region on a surface, including along the ground in an anal drag (Rasa 1973). Chew marking was the biting of vegetation and usually included at least one rapid thrash of the head. As faeces and urine were deposited at latrine sites, their inclusion as eliminative scent-marks is justified following the criteria of Kleiman (1966). Cheek marking (Rasa 1973) and body rubbing (Moran & Sorensen 1986) were not included in this study. Cheek marking is primarily involved in dominance interactions and I did not observe substrate marking with cheek glands. Previous evidence suggests that body rubs facilitate self-anointing with anal gland secretions from substrates (Moran & Sorensen 1986), and as body rubbing was primarily directed at previously scent-marked locations immediately following anal marking in this study, this seems to be a reasonable assumption. All instances of scent-marking were recorded *ad libitum*, ending when they were interrupted by a change to a different behaviour.

'*Scent-stations*' were locations that were scent-marked at least once during a latrine visit. Each was assigned a unique number, and its location was recorded onto a clear plastic sheet attached to the front of the monitor. '*Over-marking'* was the deposition of scent-marks onto existing scent-stations, and included the destruction/digging up of faeces, as this was analogous to over-marking for the questions addressed. Changes in scent-station composition throughout the latrine visit were recorded prior to detailed behavioural data collection. For each scent-mark, the scent-mark type, identity of the depositing individual, time of deposition, and scent-station number were recorded. A *'top-mark'* was the most recent scent-mark placed on a scent-station, and I assumed that each latrine was a *tabula rasa* at the onset of each latrine-visit.

3.3.3 Scent-mark investigation and over-marking patterns

Each time an individual investigated a scent-station, investigation duration was recorded to the nearest second. Only over-marking events preceded by investigation of the original scent-mark were included in analyses of over-marking to remove 'random' over-marking from our assessments of selective over-marking. Potential factors which might affect scent-mark investigation or over-marking included: scent-mark type, the age, dominance status, sex, and relative sex (relative to the recipient) of the depositing individual, and - for scent-stations with multiple scent-marks - the number of marks, and age, sex, relative sex, and dominance category of the top-mark. These factors were held constant for comparisons unless explicitly stated.

Own-mark investigation and reinforcement marking were not included in analyses, as individuals may either be differentially ‘interested’ in their own scent-marks or deposit reinforcement marks in response to an earlier scent stimulus. Eliminative and non-eliminative scent-marks were considered separately, and scent-stations containing eliminative marks were not incorporated into analyses involving multiple scent-marks, as I could not justify assigning them equal weighting with glandular secretions. Analyses were restricted to adult meerkats, as it could not be excluded that younger animals were unmotivated and/or unable to respond appropriately. It was not possible to control for sex-biases in overall scent-composition of scent-stations, and I therefore assumed that all scent-marks below the top-mark contributed equally to the composition of each scent-station.

3.3.4 Presentation experiment and sample storage

Seven dominant females and six dominant males were presented with a unique artificial latrine to investigate manipulation of latrine composition. Each presentation contained four faeces from the recipient’s own group, randomly positioned in a line on a sand-covered tray with inter-faeces distances of 8cm. In each case samples were from the dominant male, dominant female, a subordinate adult male and a subordinate adult female. An observer approached the foraging recipient and placed the artificial latrine 0.5 to 1m away. Responses were recorded on video with the tripod positioned at a distance of 1.5-3.5m. If a non-target individual approached the presentation prior to investigation by the recipient, the artificial latrine was temporarily removed and the presentation attempted again. The experiment ended when the recipient moved out of the field of view, having investigated at least one of the samples.

Faeces were collected from known individuals *ad libitum* (immediately after defecation) and transferred to individual zip-lock bags using a small plastic spoon, which was cleaned between sample collections, or with twigs that were discarded. Due to their communicatory value, only half of each sample was removed from the field. Samples were placed in a thermos flask on ice before being transferred within four hours to a deep freeze for storage at -2 to -6°C. Prior to presentation, the four experimental samples were defrosted simultaneously in the sun for 10 minutes. Samples presented to dominant males were frozen for 7.83 ± 1.43 days ($\bar{X}$ ± SE), N = 24 (range: 0-19), and 7.96 ± 1.28 days ($\bar{X}$ ± SE), N = 28 (range: 0-19), to dominant females. Samples were age-matched as much as possible within each presentation with the oldest and youngest sample differing by 0 to 8 ($\bar{X}$ ± SE = 3.83 ± 1.17) days for males, and 0 to 10 ($\bar{X}$ ± SE = 4.5 ± 1.52) days for females. The time frozen for samples from each category did not differ significantly for presentations to either sex (Kruskal-Wallis test: *male recipients,* H_3 = 0.76, P = 0.86; *female recipients,* H_3 = 0.10, P = 0.99), but whether subtle age differences were perceived by recipients is not known.

3.3.5 Statistical analyses

All statistical tests were carried out using Minitab$^{®}$ Release 12.21, or the Analyse-IT$^{®}$ extension for Microsoft Excel$^{®}$. I used parametric statistical tests unless the data was not normal (based on the Anderson-Darling test for normality). Proportional data were arcsine square root transformed to meet the equal variance and normality assumptions of ANOVA and non-proportional data were log transformed. Post hoc tests were carried out following Day & Quinn (1989). Data were paired and only incorporated into analyses when individuals investigated comparable scent-marks (i.e. from individuals of all categories of interest for comparison) during the same latrine visit. Only the first scent-marks of each specified composition that each adult individual encountered were included. For activity budget comparisons I selected the first latrine for each group where at least one individual in each demographic category of interest was present in the group at the time of latrine-use (regardless of whether they entered the latrine or not). All latrines were used in the final composition analysis.

3.4 Results

A total of 254 scent stations were identified, with 1-19 scent-stations per latrine visit ($\bar{x}$ ± SE = 7.94 ± 0.90, N = 34). 60.6% of scent-stations were marked only once during the latrine visit, with 15.7% marked twice, 9.1% three times, and 14.7% marked on four or more occasions (with up to 14 scent-marks per scent-station). Each scent-station was marked by up to five individuals during each latrine visit.

3.4.1 Latrine composition

In 32 latrine visits where at least one mark was deposited, the final latrine scent-composition did not correlate with group composition (Figure 3.1). Group size showed no correlation with either the number of scent-stations (Spearman rank correlation: $r_s = 0.038$, $N = 32$, $P = 0.84$) or the total number of scent-marks deposited in the latrine ($r_s = -0.036$, $N = 32$, $P = 0.84$). Similarly, the proportion of total scent-marks that were deposited by males showed no correlation with either the adult sex ratio ($r_s = -0.028$, $N = 33$, $P = 0.88$) or the overall sex ratio of the group ($r_s = -0.110$, $N = 33$, $P = 0.54$). The proportion of scent-stations with a male top-mark was not correlated with either the adult sex ratio of the group ($r_s = -0.068$, $N = 33$, $P = 0.71$) or the overall sex ratio of the group (r_s = -0.028, N = 33, P = 0.88). 85% (N = 33) of latrines had a male-biased final latrine composition, meaning that the majority of scent-stations had a male top-mark. In two of the five latrines where female top-marks were more common, the dominant male was either absent from the group or did not enter the latrine, and a third consisted only of a single female faeces (deposited in an existing latrine site).

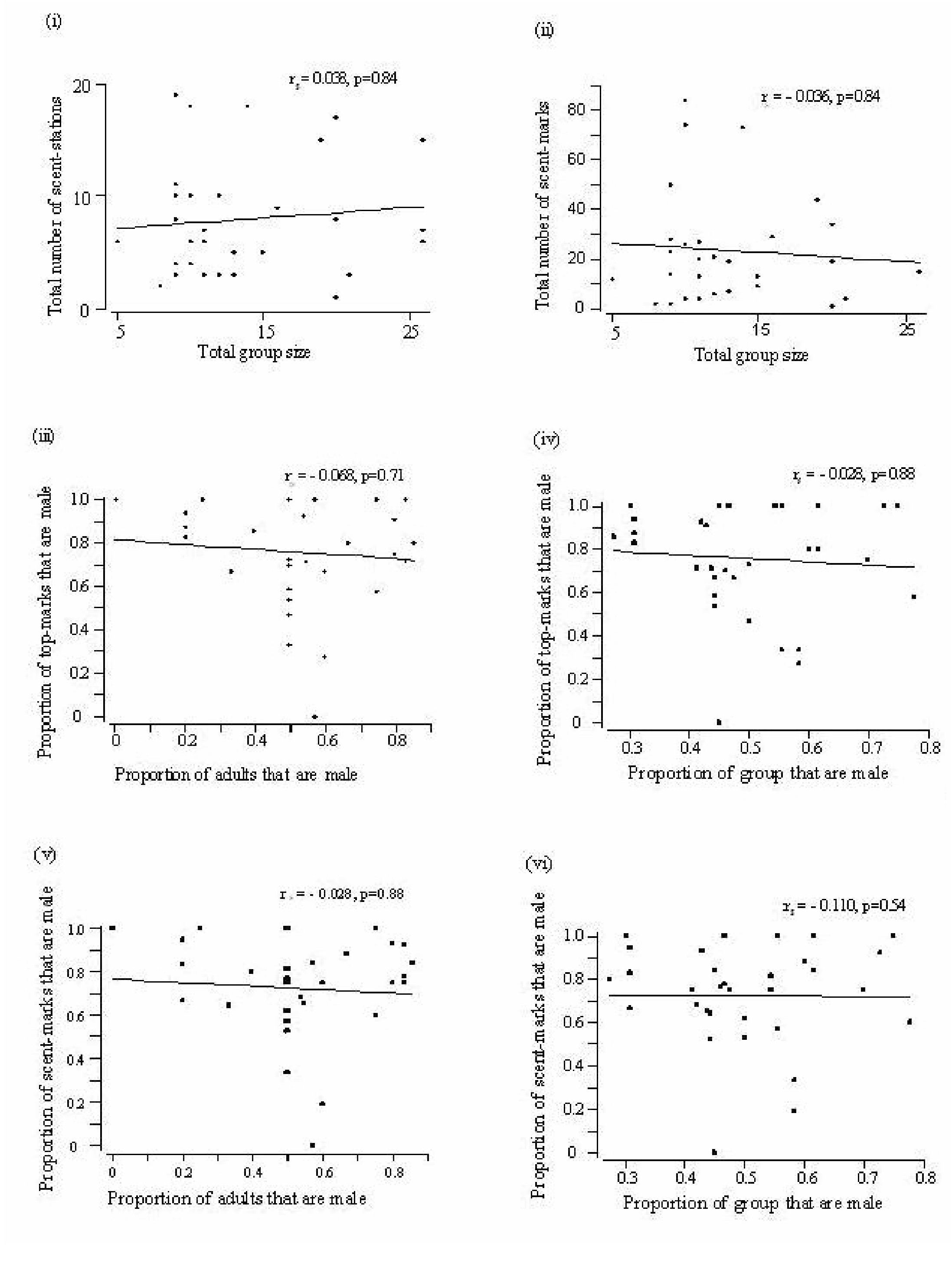
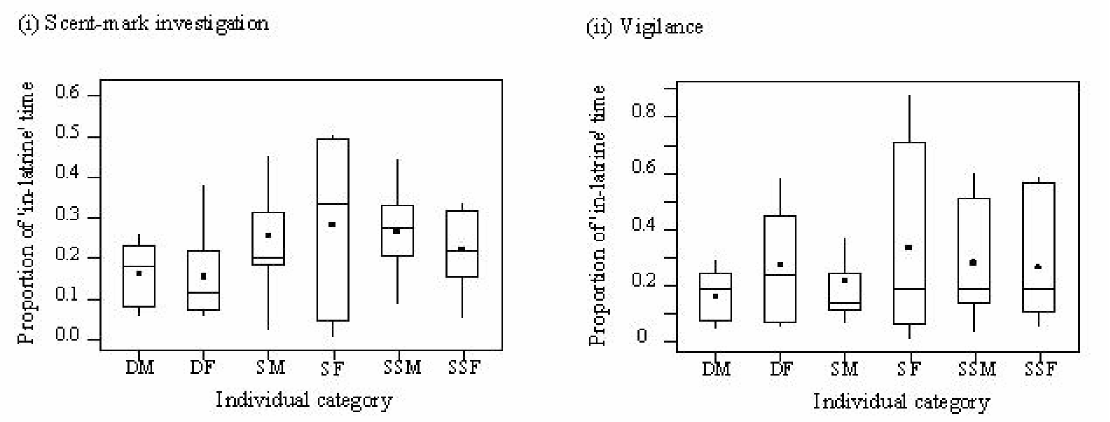


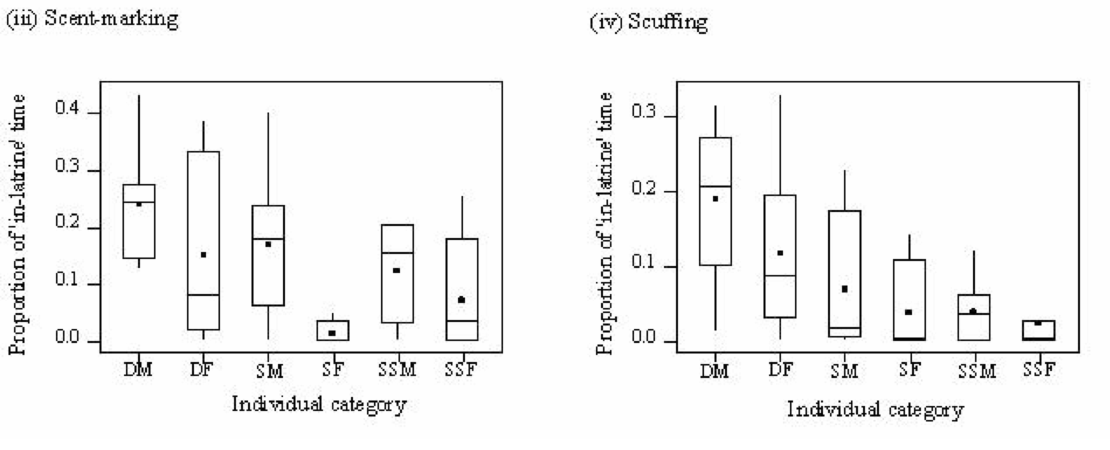
Figure 3.1. Scatter plots of (i) total group size against the total number of scent-stations; (ii) total group size against the total number of scent-marks; (iii) the proportion of adults that are male against the proportion of scent-stations with a male top-mark; (iv) the proportion of the group that are male against the proportion of scent-stations with a male top-mark; (v) the proportion of adults that are male against the proportion of scent marks made by males; and (vi) the proportion of the group that are male against the proportion of scent marks made by males. Lines are best fit, and statistics are for Spearman rank order correlations.

3.4.2 Activity budgets

The total time that individuals spent in the latrine during each group visit did not vary significantly between categories of individual (ANOVA: $F_{5,36} = 0.67$, $P = 0.65$). There was no significant difference in the proportion of in-latrine time spent investigating scent-stations or vigilant (Figure 3.2) between categories of individual (Kruskal-Wallis test: *Investigation*, H_5=6.84, $P = 0.23$; *Vigilance*, H_5=1.42, $P = 0.92$).


(i) Scent-mark investigation

(ii) Vigilance


(iii) Scent-marking

(iv) Scuffing

Figure 3.2. Box plot showing the proportion of total 'in-latrine' time different categories of individual invested in (i) scent-mark investigation; (ii) vigilance; (iii) scent-marking; and (iv) scuffing. Solid points are medians, boxes represent inter-quartile ranges, and vertical lines show the total range of values. DM=Dominant males, DF=Dominant females, SM=subordinate males, SF=subordinate females, SSM=subordinate sub-adult males, SSF=subordinate sub-adult females.

The proportion of time in the latrine that individuals spent scent-marking varied significantly with individual category (ANOVA: $F_{5, 52}$=5.71, P = <0.001). Fisher's post hoc pairwise comparison (with a significance level of $p<0.05$) showed that dominant males invested a significantly greater proportion of time scent-marking than all other categories of individual, with the exception of subordinate adult males (Fisher's pairwise test $P < 0.05$). Males from all categories invested a greater proportion of time scent-marking than females of the same category, and subordinate adult females invested significantly less in scent-marking than all other categories of individual, with the exception of subordinate sub-adult females (Fisher's pairwise test $P < 0.05$).

The proportion in-latrine time that individuals spent scuffing also varied significantly between categories of individual (ANOVA: $F_{5, 52} = 6.01$, P = <0.001). Dominant males spent a significantly higher proportion of their time scuffing than all other categories of individual except dominant females, and males from all other categories invested longer in scuffing than equivalent females (Fisher's pairwise test $P <0.05$).

3.4.3 Scent-mark investigation and over-marking patterns

Over-marking by adult meerkats was observed on 228 occasions, with 70% of over-marks preceded by investigation (sniffing) of the original mark. 43% of over-marks were reinforcement marks, with the remaining 57% placed on top-marks made by different individuals. 63% of dominant female over-marks were placed on existing scent-stations with a male top-mark (93% of which were placed on those of the dominant male). Of the remaining 37%, 87% were reinforcement marks. Dominant males placed 64% of over-marks on the existing marks of males (90% of which were reinforcement marks). Of the 36% of male over-marks on existing female marks, 79% were placed over marks from the dominant female. When reinforcement marks were removed from the dataset, dominant females placed 89% of over-marks on the existing mark of a male, and dominant males placed 86% on an existing scent-mark made by a female.

Considering single scent-marks only, there was no significant difference in time spent investigating faeces from opposite- or same- sex individuals (ANOVA: $F_{1,22} = 1.80$, $P = 0.19$), but all individuals spent a significantly greater amount of time investigating female faeces than they did male faeces (Mann-Whitney U test: $U = 110.5$, $N_1 = N_2 = 12$, $P = 0.021$). Over-marking of faeces showed a sex bias in males but not females (Figure 3.3), with 75% ($N = 16$) of all faecal over-marking by dominant males directed towards existing faeces from a member of the opposite sex, compared to 50% ($N = 12$) in dominant females. Adult males were more likely to over-mark the faeces of an adult female than the faeces of an adult male (Fishers Exact Test: $N = 26$, $P = 0.04$), but females were no more likely to over-mark the faeces of males or females ($N = 20$, $P = 0.39$).

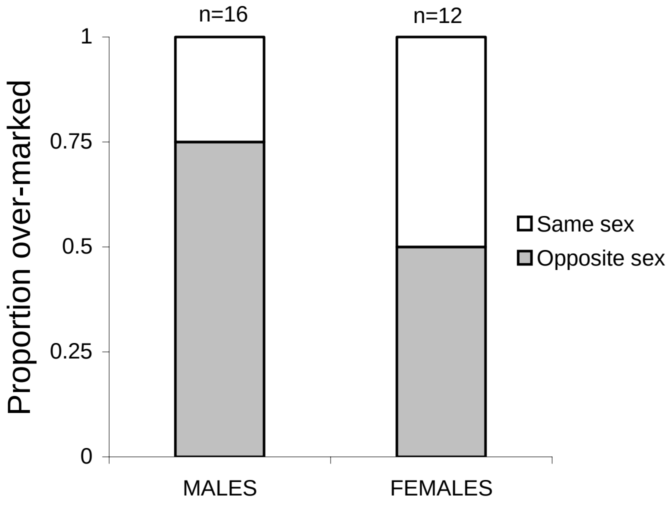


Figure 3.3. Proportion of over-marks with faeces by dominant males and females deposited on/directed at same- or opposite-sex faeces.

Due to the lower rates of non-eliminative scent-marking by all categories except dominant males, and the regular occurrence of over-marking, encounters with single non-eliminative scent-marks from females were extremely rare. It was therefore not possible to statistically compare investigation and over-marking patterns for single non-eliminative scent-marks from different sexes. However, dominant males over-marked all opposite-sex single non-eliminative scent-marks encountered ($N = 5$) compared to only 50% ($N = 4$) of scent-marks from the same-sex (Figure 3.4). Only one female scent-mark was encountered by a dominant female during the study, and this was not over-marked. Dominant females over-marked 56% ($N = 9$) of encountered male scent-marks.

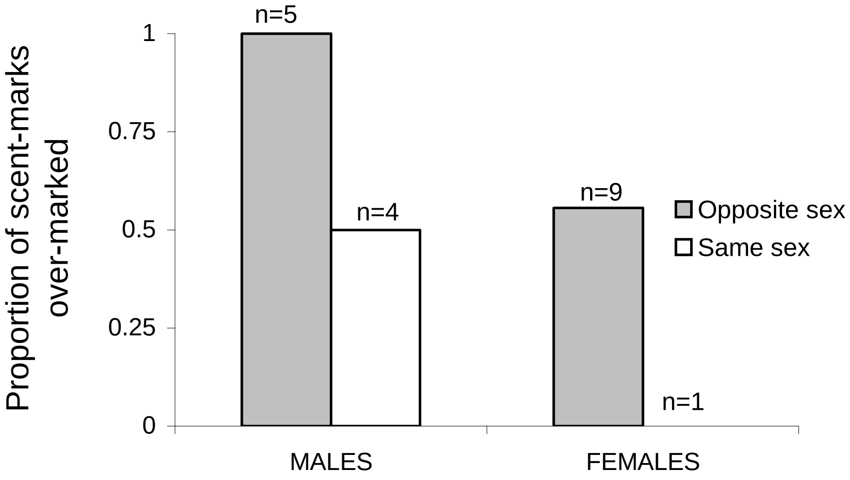


Figure 3.4. Proportion of over-marks by dominant males and females deposited on same- or opposite-sex single non-eliminative scent-marks.

The number of scent-marks on a scent-station did not affect investigation duration. Adult individuals spent similar amounts of time investigating scent-stations with either one, two or three anal marks when they encountered at least one of each complexity during a single latrine visit (Kruskal-Wallis test: H_2=2.30, P = 0.32).

Males were significantly more likely to over-mark scent-stations with an opposite-sex top-mark than scent-stations with a same-sex top-mark (Fisher exact test: N = 26, P < 0.01). Importantly, males over-marked scent-stations with opposite-sex top-marks on 93% of encounters (N = 14) compared to only 33% for scent-stations with same-sex top-marks (N = 12) (Figure 3.5). Only one dominant female encountered a scent-station with a (non-self) same-sex top-mark, and this was over-marked. Dominant females over-marked opposite-sex top-marks on 73.3% of occasions (N = 15).

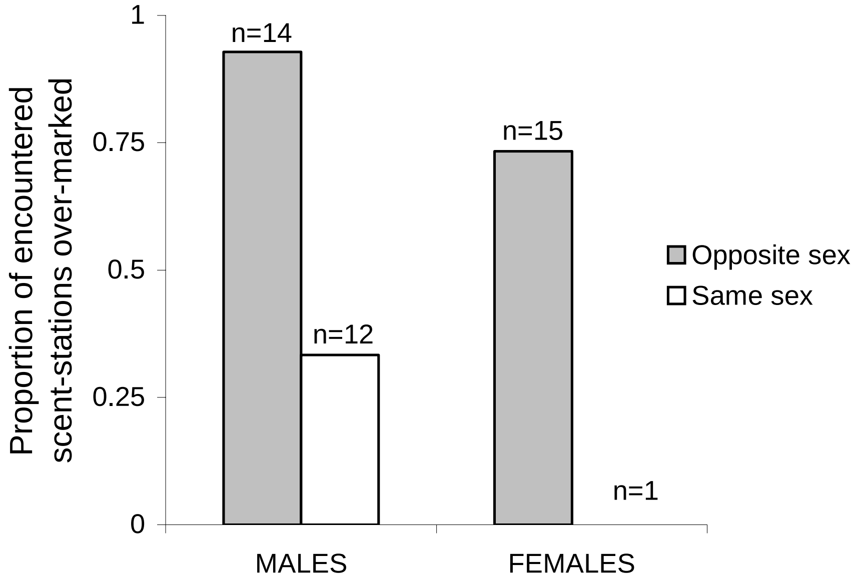


Figure 3.5. Proportion of over-marks by adult males and females deposited on all same- or opposite-sex scent-stations with non-eliminative scent-marks.

3.4.4 Experimental presentations

Six separate presentations were made to dominant individuals of each sex, which was the largest sample size possible as constrained by faecal sample availability. Manipulation of latrine composition by the target individual occurred in two of the six presentations to dominant males. In one instance the dominant male destroyed the dominant females' faeces; in the second an anal mark was placed on it, and the surrounding vegetation was anal and chew marked.

All faeces were investigated during most - but not all - presentations (3/6 presentations to males; 4/6 presentations to females). Both recipient types invested more time sniffing the faeces of dominant females than all other categories (Figure 3.6). Sample size did not allow statistical comparison, but general investigative trends fit those described during natural observations.

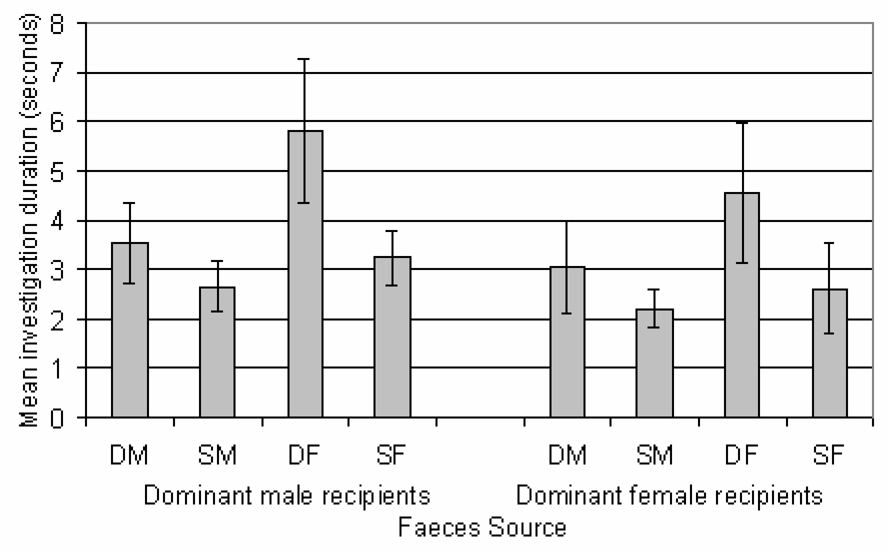


Figure 3.6. Investigation duration (s) for faecal samples from dominant males (DM), subordinate males (SM), dominant females (DF) and subordinate females (SF), during latrine presentations to dominant males (left) and dominant females (right). Error bars represent standard errors.

3.5 Discussion

In common with previous descriptions of territory defence, meerkat males invested more than females in scent-marking at latrine sites. This suggests that mates and not food are the defended resource, and is consistent with patterns of scent-marking observed in previous studies of meerkats (Gsell 2002) and carnivores in general (for a review see Macdonald 1980). Males were more likely to over-mark both the faeces of females and scent-stations with a female top-mark, which suggests that males disguise the presence of females, or at least advertise a commitment to defend them. This mate-defence function was previously suggested for European badger latrines (Roper et al. 1986), but remains unexplored in that species. In contrast, although females spent a similar amount of time in latrines, they scent-marked significantly less and did not selectively over-mark. Females invested a significant proportion of time investigating scent-marks, and sniffed the scent-marks of females for significantly longer than the scent-marks of males. This suggests that females enter latrines to assess the reproductive status of other resident females, and do not invest heavily in latrine production or maintenance.

This study found no correlation between latrine and group composition, as the final scent-mark composition of latrines was almost always male-biased when males were present in the group. Although meerkat latrine composition did not provide a reliable signal of either group size or demography, more basic information may be obtained from latrines. For example, extra-group males could assess and respond to an absence of males in an encountered or neighbouring group by an absence of male scent-marks at latrine sites. Additionally, as latrine-use often occurs in direct response to encounters with prospecting males (Chapter 2), visual observation of this almost sexually dimorphic behaviour might allow an assessment of group composition prior to committing to a costly approach. Scent-marking is costly, especially where deposits contain constituents of large molecular weight (Gosling et al. 2000), and the negative impact on condition is generally assumed (Alberts 1992; Rich & Hurst 1998). Scent-marking frequency could therefore indicate fitness, and dominant males may be sexually selected to scent-mark at high rates. Therefore, although accurate group composition could not be determined by olfactory cues at latrine sites, visits may still provide valuable information for dispersing meerkats.

That prospecting males are the intended recipients of latrines is supported by observations that meerkat latrine-use is stimulated by the presence of extra-group males (Chapter 2), and that prospecting males spend a considerable amount of time investigating latrines during intrusions (personal observations). Latrines are located in proximity to refuge (Chapter 2), and this increases the likelihood of detection, as prospecting males travel from refuge to refuge (Doolan & Macdonald 1996). The efficacy of intruder interception by latrines may be further increased by visual cues, which direct intruders nearby to the latrine site (see Roberts & Gosling 2001 for other examples). Scuffing behaviour was more frequent in males than females, and resulted in the creation of a large number of characteristic pits. These pits were obvious to human observers from much further away than the average latrine-refuge distance, and may therefore facilitate effective local orientation to the site. However, it is also possible that meerkats possess inter-digital glands, and that scuffing is involved in scent-marking, as was demonstrated for aardwolves (Stoeckelhuber et al. 2000). If this is the case, latrines were even more male-biased than described here.

Although females spent a similar amount of time as males in latrines, they scent-marked significantly less, and were no more likely to over-mark an existing faeces from either sex. However, this does not indicate a lack of interest in latrine sites, as individuals of all categories spent similar proportions of time investigating scent-stations, with subordinate females actually investigating scent-marks for marginally longer than all other categories. If male and female scent-marks are equally likely to repel prospecting males, this lack of marking might indicate a lack of motivation in this regard. However, as many species can discriminate faeces on the basis of sex (e.g. domestic dogs, Dunbar 1977; meerkats, Gsell 2002), and all meerkats spent longer investigating the faeces of females in this study, it seems reasonable to interpret that they are able to differentiate between the sexes by scent. Indeed, in many species it is possible to determine sex and reproductive status of individuals by quantifying metabolites of sex-steroids excreted in faeces and/or urine (Heisterman et al. 1995), and members of several carnivores use urine and or faeces as reliable advertisement signals in the context of reproduction (Brown & Macdonald 1985). It also follows that scent-marks from the two sexes are likely to elicit different responses in recipients, but further experiments are necessary to determine the responses of prospecting males to scent-marks of each sex. Although it is possible that males do not assess group composition at all, two anecdotal observations of extra-group males entering latrines containing only male scent-marks support this view. Following investigation, these males immediately retreated to their resident group in both cases, suggesting that composition assessment is occurring. Further controlled experiments are required to assess the responses of prospecting males to latrines of mixed composition.

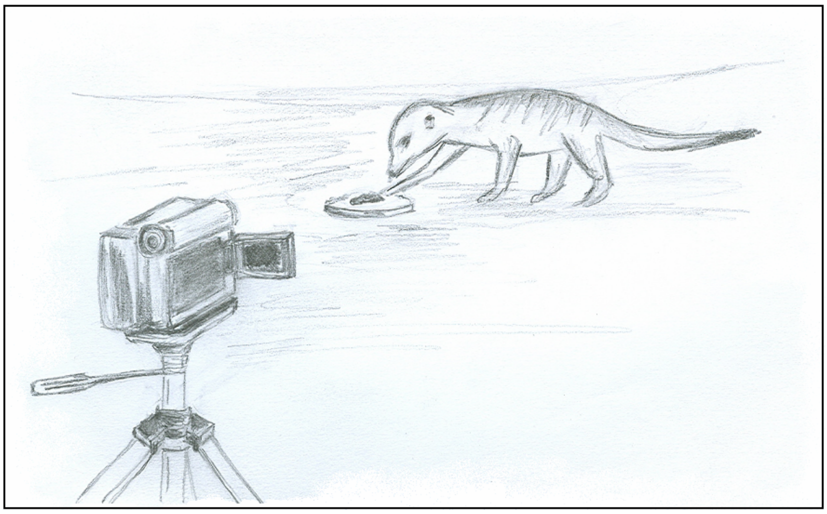
Patterns of scent-marking by females were not consistent with either a mate-defence or mate-advertisement function for female latrine-use. Females did not selectively over-mark male faeces, and scent-marking rates were significantly lower than age- and dominance- matched males. In common with territoriality in general, latrine behaviour may serve different functions in the two sexes, and a commonly cited hypothesis is that latrines serve to signal food defence (e.g. spotted hyaena, Bearder & Randall 1978; striped hyaena, Macdonald 1978; grey fox, Trapp 1978). However, if latrines were responsible for the defence of energetic resources, then one would expect females to invest equally or to a greater extent than males, as the energy requirements of females are greater. Alternatively, females may accrue benefits through an intra-group communicatory function (Ralls 1971). Although individuals showed no significant difference in the time they spent investigating same- or opposite- sex faeces, all individuals spent significantly longer investigating female faeces. Due to high levels of reproductive skew in meerkat groups, group activities are profoundly influenced by the breeding status of dominant females. Although acquisition of information on female breeding status would therefore benefit all group members, subordinate females are expelled from the group in the latter stage of the dominant's pregnancy (Clutton-Brock et al. 1998a) and so might benefit most if they could adjust their behaviour and avoid expulsion. Additionally, dominant females would gain by monitoring the status of subordinates, as dominants are more likely to evict pregnant subordinates (Young 2003). This presumably reduces reproductive conflict within the group, as evicted females were significantly more likely to abort than females that were not evicted (Young 2003).

Dominant females may mate with prospecting males without affecting the helping effort of resident subordinates, as contributions to cooperation are not kin-biased in meerkats (Clutton-Brock et al. 2001a). However, dominant females may incur indirect costs by allowing unrelated males to interact with subordinate females. As all of our study groups consisted of a mother and her subordinate offspring, reproductive conflict will be substantially lower if the current dominant male is retained, since he is a potential mate for the dominant female only. By encouraging immigration by advertising to unrelated males at latrine sites, dominant females may increase the likelihood of subordinate pregnancies and as intra-group reproductive conflict increased, so the reproductive success of the dominant female would be expected to decrease. However, information about the response of prospecting males to female scent-marks is required, as these could have either an encouraging or repelling effect on prospectors.

Meerkat behaviour at latrines was consistent with the hypothesis that latrine function is sexually dimorphic, in common with territoriality for carnivores in general (e.g. African lions, Packer et al. 1990; Grinnell et al. 1995; Heinson & Packer 1995; Boydston et al. 2001). Strategies for maximising reproductive success are commonly sexually dimorphic (Clutton-Brock 1988), but this is further complicated in cooperative societies where intense reproductive conflict results in diverse costs and benefits to intruder deterrence. Since the presence of prospectors results in a differential threat to different group members, latrine behaviour may be better explained as serving selfish interests rather than cooperative defence. Whereas male meerkat behaviour fits the hypothesis that latrine-use is involved in mate-defence, lower scent-marking investment and non-selective over-marking by females suggest that they do not visit latrines to deter (or even attract) prospecting males. Instead, females may benefit from latrine visits by assessing the reproductive status of other females, which has a profound effect on their own survival and reproductive success.

4

Do meerkats exhibit olfactory kin-discrimination?



Prepared in accordance with guidelines for submission to the journal Animal Behaviour

4.1 Abstract

Kin discrimination describes a differential behavioural response towards kin versus non-kin, and is potentially adaptive in a wide range of circumstances. Despite the fact that many mammals rely heavily on scent, the role of olfaction in kin discrimination has received relatively little attention. Cooperative meerkats, *Suricata suricatta*, exhibit high reproductive skew and relatively long dominance tenures for both sexes, and so unfamiliar siblings have a high probability of encountering one another post-dispersal. Under such circumstances, selection for remote kin discrimination by olfactory means should be expected in order to avoid breeding with close relatives. In this preliminary assessment of olfactory discrimination, meerkats did not appear to discriminate between faeces on the basis of kinship. Although recipients were more likely to give recruitment calls in response to foreign faeces than to faeces from their own group, faeces from extra-group individuals differing in relatedness to recipients - but not in familiarity- were investigated for similar durations and were equally likely to evoke vocal recruitment. These results suggest that individuals are able to discriminate faeces of individuals on the basis of group membership but not kinship. The results of this preliminary study are discussed in the context of kin selection and discrimination theory.

4.2 Introduction

Kin selection theory predicts that genetic relatedness should influence social relationships, because animals interacting differently with kin and non-kin would have higher inclusive fitness than those not doing so (Hamilton 1964). Such a differential behavioural response towards kin is called kin discrimination (Tang-Martinez 2001), and both the occurrence of nepotism (Hamilton 1987; Mateo 2002) and observations that relatedness is an important criterion in mate choice (Smith 1979; Hoogland 1982; Shields 1982, 1983; Bateson 1983, 1988; Partridge 1983), suggest that kin discrimination is widespread.

Most studies of kin discrimination conclude that individuals have to learn about kin in order to discriminate between them (Hepper 1991). Individuals must therefore ensure that the information they use is derived from relatives, and this is generally assumed to occur by one of two main mechanisms. In the first, kin discrimination results from ‘familiarity’, where kin may learn to recognise each other by interacting in contexts that vary with relatedness. For example, siblings born in different breeding seasons may recognise each other as kin through shared association with a common parent (e.g. Dawkins 1982). Secondly, ‘phenotype matching’ (Holmes & Sherman 1982) describes the process whereby an individual learns its own phenotype(s) and/or those of its familiar kin, and stores these as a ‘kin template’. This template is later retrieved and compared to the phenotypes of unidentified individuals (see also Sherman et al. 1997). This second mechanism requires a relationship between phenotypic and genotypic similarity, so that conspecifics that display traits most closely matching an individual’s template are its closest kin (Mateo & Johnston 2000). In this context, a feasible and direct mechanism would be to match rare alleles at one or a few loci, which are likely to be shared only by close kin (Grafen 1990). Such highly polymorphic loci include those involved in the major histocompatibility complex (MHC), and evidence suggests that they may be involved in mate choice in a number of vertebrates (e.g. house mice, *Mus domesticus,* Yamazaki et al. 1976, 1978; humans, Wedekind et al. 1995; Wedekind & Füri 1997; three-spined sticklebacks, *Gasterosteus aculeatus,* Milinski 2003; or for a review see Jordan & Bruford 1998). The notion that early experience affects subsequent MHC-based mate choice is supported by cross-fostering experiments on house mice (Beauchamp et al. 1988; Yamazaki et al. 1988).

Depending on the social system of the species in question, individuals may have access to relatives or may have to refer to their own phenotype to facilitate subsequent matching. The so-called 'armpit effect' (Dawkins 1982) describes self-referent phenotype matching, where individuals learn and use their own phenotypes as templates to compare to potential relatives. This enables the most accurate assessment of kinship, since an individual's own cues will more accurately reflect its own genotype than cues of close kin (Mateo & Johnston 2000). Self-assessment and subsequent matching should be favoured in species with multiple maternity and/or paternity, or when individuals commonly encounter siblings post-dispersal (Holmes & Sherman 1982; Holmes 1986; Sherman 1991).

Meerkats are obligate cooperative breeding herpestids, living in groups of 2-49 individuals (Clutton-Brock unpublished data). Groups commonly consist of a dominant breeding pair and their offspring, which remain in their natal group past sexual maturity and assist their parents to rear subsequent litters (e.g. Doolan & Macdonald 1997; Clutton-Brock et al. 1999a, b; Clutton-Brock et al. 2001a). Both males (voluntarily) and females (forced) disperse post-maturity, either individually or in coalitions (Doolan & Macdonald 1996; Clutton-Brock et al. 1999a). Males generally immigrate into established groups by usurping resident males, whereas evicted females may form new groups with unrelated males (Young 2003). Prior to permanent dispersal, males engage in extra-territorial prospecting forays to nearby groups, where they attempt to mate with unrelated females and possibly assess dispersal opportunities (Young 2003). Such forays are energetically expensive, and potentially fatal, as resident males will often chase and sometimes kill prospectors (Young 2003). Given high levels of reproductive skew and relatively long dominance tenures for both sexes, unfamiliar siblings from different litters may be encountered relatively frequently outside the natal territory.

Here I aim to make a preliminary assessment of the kin discriminatory abilities of meerkats in a natural context. I concentrate on subordinate male meerkats, as males disperse into existing groups where assessment of kinship prior to an approach would be advantageous. Where target groups contain female close kin, the costs of prospecting probably outweigh the potential reproductive benefits, as close inbreeding is generally avoided (Hoogland 1982; Bateson 1983). As latrines are stimulated by the presence of prospectors (Chapter 1), and prospectors spend considerable amount of time investigating latrines (personal observation), olfactory kin discrimination could occur at these sites. Since non-eliminative scent-marking by females is relatively rare (Chapter 2), and faeces are a common source of individual odour (for review see Halpin 1980), I focus on faeces and conduct a presentation experiment to assess the ability of recipients to discriminate between faeces of related and unrelated individuals of equal (un)familiarity.

4.3 Methods

4.3.1 Study area and population

I undertook this study between October 2003 and December 2004 on recovering ‘ranchland’ in the southern Kalahari, 29km west of Van Zylsrus in South Africa’s Northern Cape (28°58’S, 21°49’E). I collected data from twelve groups of wild meerkats, habituated to close human observation and handling. All individual meerkats were given a small hair-dye mark on their pelage to allow rapid field identification, and one individual in each group was fitted with a radiocollar (Sirtrack®). Further details of the study site are given previously (Clutton-Brock et al. 1999c). The age of over 95% of all study individuals was accurately known (usually to the nearest day, but no more than three days out) as they had been followed since birth. The genetic composition of the population is well known: maternal identity was easily assigned by weight loss on parturition, and paternity was derived based on 12 variable micro-satellite loci, combined with the identity of the mother and the likely father (Griffin et al. 2003; Spong unpublished data).

4.3.2 Data collection

Olfactory self-assessment was recorded as a sniffing bout directed at the individuals own faeces immediately post-defecation. In such circumstances, the individual normally turns around and directs one or two sniffing bouts at it’s own faeces, lasting from about one to nine seconds. I investigated whether this was more likely at particular ages and/or times of year. For each observed defecation (N = 2148 defecations from 312 individuals), I recorded whether olfactory self-assessment occurred. To ensure independence of data points, one observation of defecation was randomly extracted for each individual. Males and females were analysed separately, to allow for the possibility that this behaviour was sexually dimorphic.

4.3.3 Discrimination experiment

Faeces were collected from known individuals *ad libitum* throughout the study. Due to their role in communication only half of each sample was removed from the field. A small plastic spoon or twig was used to transfer faeces into individually labelled zip-lock bags, and the spoon was cleaned between sample collections. Samples were placed in a thermos flask on ice before being transferred to a deep freeze for storage at -2 to -6°C. Presented samples were 8.4 ± 2.61 ($\bar{X}$ ± SE) days old (range: 0-44) for dominant females, 9 ± 2.26 ($\bar{X}$ ± SE) days old (range: 0-42) for dominant males and 4.7 ± 0.56 ($\bar{X}$ ± SE) days old (range: 1-11) for subordinate males. Samples were age matched as much as possible in each presentation, and samples from each kinship category did not differ significantly in age when presented to dominant females (Kruskal-Wallis test: H_2=1.24, P = 0.54), dominant males (H_2=0.34, P = 0.84), or subordinate males (H_2 = 3.39, P = 0.18). Each sample was transported in a thermos and defrosted for 10-minutes prior to presentation, and placed onto a metal jar lid covered with sand collected from the presentation site.

20 subordinate adult philopatric males from 10 groups were each presented with three samples at 10-minute intervals. If a non-target individual approached the presentation prior to investigation by the recipient, the faeces was temporarily removed and the process began again. The experiment was deemed complete when the recipient moved >1m from the presentation after investigating the sample. Presentation order was randomly determined in each case with samples presented from: a group member

(sample "G"), and two non-group members that where either related (sample "R") or unrelated (sample "U") to the individual who produced sample G. In each presentation, samples R and U originated from individuals of the same age, sex and dominance class as individual G. Wherever possible, sample R was selected from an individual born into the same litter as individual G, but when this was not possible, these samples were taken from half siblings (related maternally). To control for familiarity, samples R and U were taken from groups that either both neighboured or did not neighbour the recipient's group, where neighbours were defined as sharing overlapping home ranges at the 95% kernel derived using the LSCV value for H in Arcview® (ESRI) (see Chapter 2 for details). Recipient responses were recorded using either a Sony CCD-TRV46E analogue camcorder or Sony DCR-PC120E digital camcorder mounted on a Starfoto® tripod, 52cm above ground level. Sound recordings were made with an ME66 Sennheiser® directional microphone with K6 module connected to the camcorder and attached to the tripod. The total time that recipients spent investigating the presented faeces was recorded in seconds from the videos. When individuals interrupted investigation but did not leave the vicinity (>1 metre) before reinvestigating the faeces, the combined time investigating the faeces was recorded. Meerkats emit alarm-like vocalisations in response to faecal samples of foreign meerkats, and these calls cause a response in other group members similar to that shown when they encounter snakes: other group members are recruited to the caller to investigate deposits in the same way as they join a caller to mob a snake (Manser 2001). The presence or absence of these 'recruitment' calls was noted for each presentation.

4.3.4 Statistical analysis

All statistical tests were carried out using Minitab® Release 12.21, or the Analyse-IT® extension for Microsoft Excel®. Parametric statistical tests were used unless the data differed significantly from normal (based on the Anderson-Darling test for normality), in which case they were log transformed. Where transformation was unsuccessful, equivalent non-parametric statistics were used.

4.4 Results

Age had a significant effect on the likelihood of olfactory self-assessment for females but not males, and the time of year had no significant effect on self-assessment for either sex (Table 4.1).

Table 4.1. Binary logistic regression showing Odds Ratio's (OR) and 95% confidence intervals (CI) for males and females.

Sex	**Predictor**	**n**	**OR (95%CI)**	**P value**	**Significance**
Males	Month of year	156	1.02 (0.91-1.14)	0.720	NS
	Age (days)	156	1.05 (0.96-1.16)	0.270	NS
Females	Month of year	155	1.02 (0.91-1.14)	0.752	NS
	Age (days)	155	0.89 (0.79-0.99)	0.038	*

Olfactory self-assessment peaked at 12-months of age for females (Figure 4.1), which coincides with the onset of directed aggression from the dominant female (Clutton-Brock et al. 1998a). The time of year had no significant effect on the likelihood of olfactory self-assessment for either sex (Figure 4.1).

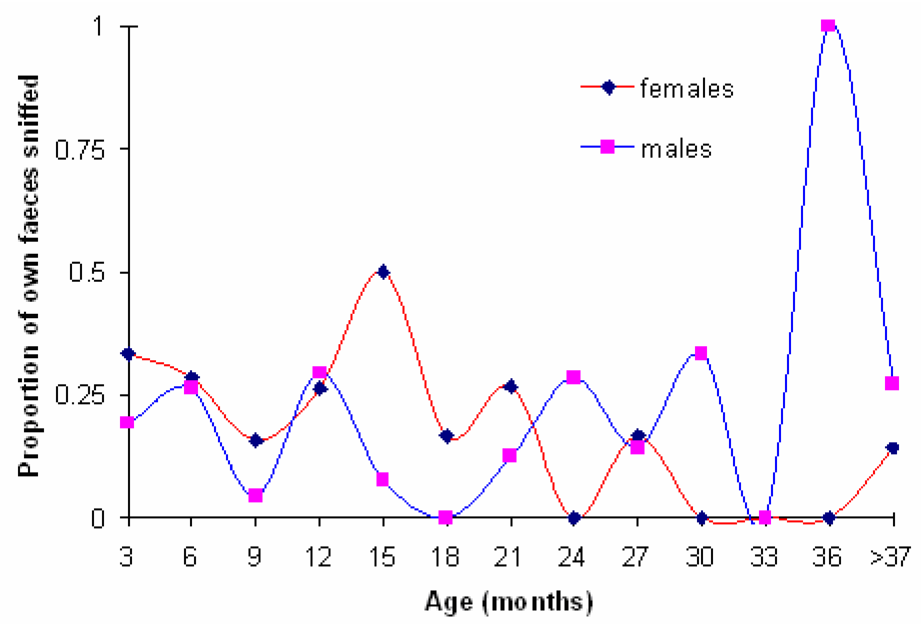


Figure 4.1. The proportion of faeces that were sniffed by males (—■—) and females (—◆—) during three-month periods (upper age in months plotted for preceding three month period).

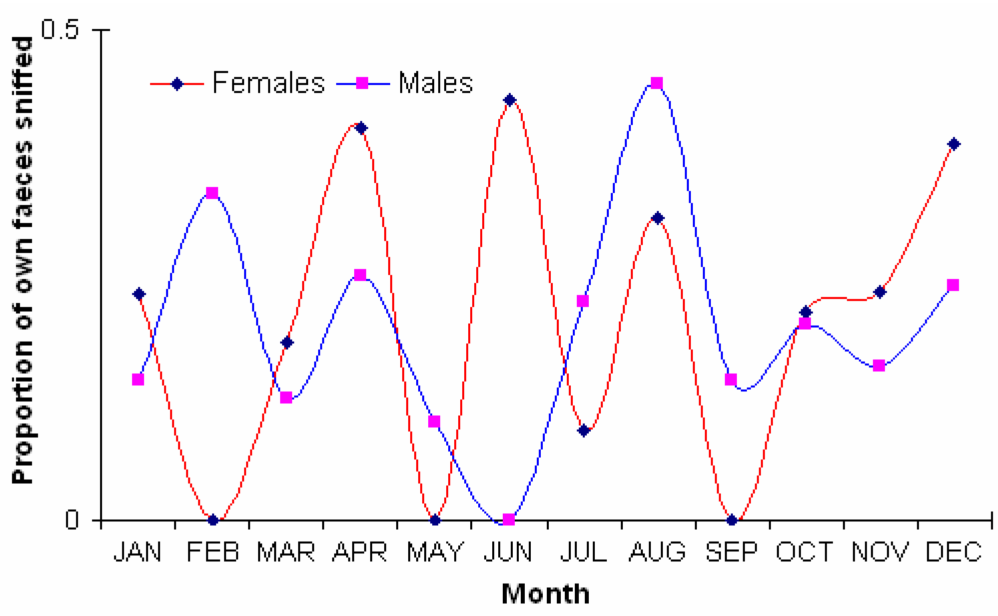


Figure 4.2. The proportion of faeces that were sniffed by males (—■—) and females (—◆—) during each calendar month.

In experimental presentations, recipients spent no longer investigating the faeces of unrelated non-group (U), related non-group (R) or own-group (G) individuals of any category (Figure 4.3) (Kruskal-Wallis test: *dominant male faeces*, $H_2 = 2.21$, $P = 0.33$; *dominant female faeces*, $H_2 = 1.08$, $P = 0.58$; *subordinate male faeces*, $H_2 = 0.75$, $P = 0.69$). This result held when familiarity was controlled for by removing the response to the 'G' faeces (that originating from the same group as the recipient) from analyses (to control for familiarity): recipients spent no longer investigating the faeces of either extra-group related or unrelated females (Mann-Whitney U test: *dominant male faeces*, $U = 61.5$, $N_1=N_2=7$, $P = 0.28$; *dominant female faeces*, $U = 33.5$, $N_1=N_2=6$, $P = 0.42$; *subordinate males*, $U = 48$, $N_1=N_2=7$, $P = 0.61$).

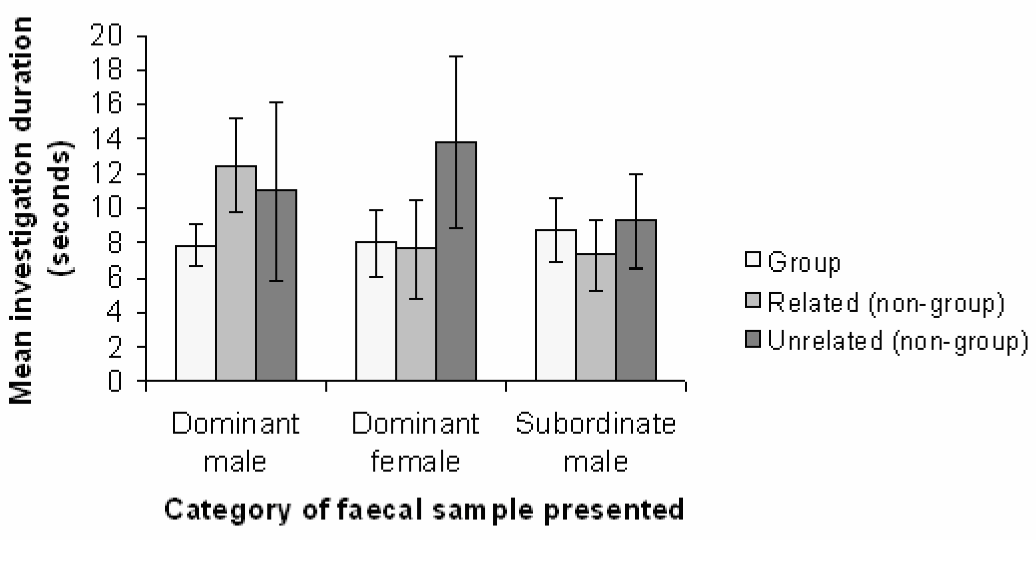


Figure 4.3. The mean investigation duration (seconds) of faecal samples presented to subordinate philopatric natal males, shown with standard error bars. Samples presented were from a group member, a related non-group member and an unrelated non-group member of each of three sex/dominance classes (dominant males ($N = 7$), dominant females ($N = 6$) and subordinate males ($N = 7$)).

The emission of at least one ‘recruitment’ call during investigation did not depend on kinship factors of the faeces presented for either subordinate male faeces or dominant female faeces, but it was statistically significant for the faeces of dominant males (Table 4.2). Subordinate adult philopatric males were more likely to give recruitment vocalisations in response to the presentation of faeces from related non-group dominant males compared to their own group dominant males and unrelated non-group dominant males.

Table 4.2. Presence (Yes) or absence (No) of a vocal ‘recruitment call’ response by subordinate adult philopatric males to matched presented faeces from a group member (G), and non-group members of equal familiarity that were either related (R) or unrelated (U) to the presented group member. Faeces were from the same category (either subordinate male, dominant female or dominant male) in each presentation.

Presented faeces category	Trial	**Vocal response given?**			Cochran’s Q test
		G	**R**	**U**	
Subordinate male	1	No	Yes	No	*Q = 2* *P = 0.37 (NS)*
	2	No	No	Yes	
	3	No	No	No	
	4	No	Yes	No	
	5	No	No	No	
	6	No	No	Yes	
	7	Yes	Yes	Yes	
Dominant female	1	No	No	Yes	*Q = 4.47* *P = 0.097 (NS)*
	2	No	No	No	
	3	No	Yes	Yes	
	4	No	No	No	
	5	No	No	No	
	6	No	No	Yes	
Dominant male	1	No	Yes	No	*Q = 6.5* *P = 0.039 (*)*
	2	No	Yes	Yes	
	3	No	Yes	No	
	4	No	Yes	No	
	5	No	No	No	
	6	No	No	No	
	7	Yes	Yes	Yes	

Only 10% (*N* = 20) of all presentations of the faeces of group members (G) elicited a vocal recruitment response in recipients, compared to 45% of presentations of faeces from related non-group members (R), and 40% of presentations of faeces from unrelated non-group members (U).

As familiarity may explain the low response to group members faeces, I then compared the vocal responses given to R and U samples only (using the raw data presented in Table 4.2 from columns R and U). On presentation of extra-group faeces, the presence or absence of a recruitment vocalisation response did not depend on the relatedness of the faeces to a member of the recipient's group. Faeces from extra-group related individuals were equally likely to evoke vocalisations as faeces from extra-group unrelated individuals (McNemar change test: *dominant male faeces*, *N* = 7, *P* = 0.25; *dominant female faeces*, *N* = 6, *P* = 0.5; *subordinate male faeces*, *N* = 7, *P* = 1.0).

4.5 Discussion

Meerkats did not appear to discriminate between faeces on the basis of kinship. Faeces derived from extra-group individuals, differing in relatedness to recipients but of equal familiarity, were investigated for similar durations and were equally likely to evoke a vocal recruitment response. However, whereas only 10% of all presentations of a (same) group member's faeces elicited a vocal recruitment response, 45% of faeces from related non-group members, and 40% from unrelated non-group members, elicited vocal recruitment responses. Recipients were significantly less likely to give recruitment calls in response to faeces from their own dominant male compared to faeces from extra-group dominant males. Similarly, recruitment vocalisations were more frequently emitted in response to faeces from an extra-group dominant female compared to their own dominant female, but this was marginally insignificant. These results suggest that individuals are able to discriminate faeces of dominant individuals on the basis of group membership, but not kinship.

Previous studies on mammals indicate that cues from familiar and unfamiliar individuals are treated differently (e.g. African dwarf mongoose, Rasa 1973; Mongolian gerbil, *Meriones unguiculatus*, Halpin 1976; domestic dog, Dunbar & Carmichael 1981; Columbian ground squirrel, *Spermophilus columbianus*, Harris & Murie 1982). Although this means that one cannot assume that familiarity has no effect (Halpin 1986), few studies have compared responses to cues of equal familiarity (for an exception see Müller-Schwarze & Müller-Schwarze 1972). In contrast to these studies I compared responses to faeces of equal familiarity - but differing in kinship - to the recipient. The results presented here showed no significant difference in responses to dominant female, dominant male or subordinate male faeces on the basis of kinship. This suggests that kinship did not influence the response of meerkats to foreign faeces, but that either group membership or familiarity explained the patterns of olfactory discrimination observed.

That meerkats did not discriminate faeces on the basis of kinship is perhaps surprising, as there are a number of contexts where gathering remote olfactory information of this kind would be advantageous. However, discrimination may be context dependent, and as all presentations were conducted to subordinate adult males within their own territory, these results are context limited. It could be argued that familiarity is the most important factor upon which responses should be based in the tested context. As dominant individuals do not leave their own group individually, the presence of their faeces is a reliable indicator of incursions from neighbouring or transient groups and so may indicate an imminent threat to territorial ownership or to loss of space. As there is no direct evidence to suggest that kinship affects territoriality in mammals (e.g. African lion, Spong & Creel 2004), the recognition of faeces merely as foreign would be sufficient in this context, as foreign dominants on the territory present an equal threat irrespective of kinship.

Situations more likely to involve decisions based on kinship are those associated with reproduction. In contrast to kin selection theory (Hamilton 1964), meerkats do not direct helping effort towards close kin (Clutton-Brock et al. 2001a), but do breed preferentially with non-relatives (Griffin et al. 2003). This could be facilitated by following a simple proximate mechanism that relied on an external referent, for example spatially based recognition (Sherman & Holmes 1985), but cage experiments (Clutton-Brock unpublished data) and natural observations (Young personal communication) showing that meetings between opposite-sex relatives outside the natal territory do not result in mating, suggest a more complex explanation. However, as these situations involved individuals that were also familiar with one other, one cannot discount the possibility that mating decisions are also related to familiarity. Additional experiments on olfactory discrimination in extra-territorial mating contexts would be a logical extension of this study.

As recognition is an unobservable neural process (Tang-Martinez 2001), it is not possible to demonstrate whether meerkats are able to *recognise* kinship from faeces, but on the basis of their observed responses to these different stimuli, meerkats either do not or cannot *discriminate* on this basis. As Beecher (1991) points out, a failure of discrimination could imply either that discrimination is not possible (due to recognition failure), or not adaptive in the specific circumstances. As I necessarily measured only behavioural responses, I cannot discount the possibility that individuals may recognise differences but treat them similarly, as failure of discrimination does not demonstrate failure of recognition (Tang-Martinez 2001). In common with previous discussions and experiments, I have focused on the identification and perception aspects of discrimination only. Failure to discriminate could therefore reflect conservative decision making rather than perceptual inability.

In contrast to dominant samples, the faeces of subordinate males were treated similarly, regardless of either group membership or kinship. This is perhaps surprising, as the presence of extra-group prospecting males is potentially deleterious to resident males, as prospectors may successfully breed with the dominant female (Griffin et al. 2003), or immigrate permanently into the group (Young 2003). As a result resident subordinate males may contribute to raising less related offspring or be permanently displaced from the group respectively. However, as prospecting males behave conspicuously when approaching a group and are easily identified by this behaviour even by human observers (personal observations), the selective pressure for remote olfactory discrimination may not exist in this context. Once again, it is not possible to differentiate between failure at the recognition or discrimination level. Furthermore, as prospectors fairly commonly pass through territories on their way to other groups, the presence of foreign subordinate male faeces on territories does not reliably signal a current threat. The dissemination of and response to signals from relatively long lasting cues (in this case faeces) might not be expected when accurate visual signals coinciding with the threat are available.

Olfactory self-assessment was correlated with age in females, and reached a peak at twelve-months. As female dispersal commonly occurs at this age, so the likelihood of encountering unfamiliar conspecifics increases. Although such a correlation is suggestive of self-referential phenotype matching, one cannot of course test this hypothesis explicitly in a socially living species because to do so individuals must be deprived of relatives (Hauber & Sherman 2001). Additionally, in a highly social species such as meerkats, both self-referent matching and assessment of the scent of relatives probably contribute to the individual's olfactory template. In such multi-paternity and multi-maternity systems, it is expected that cues from relatives are included in this template (e.g. Penn & Potts 1998). The lack of age-dependent olfactory self-assessment in males however seems to invalidate the suggestion that meerkats display self-referent matching, as males also engage in extra-territorial forays at this age (Doolan & Macdonald 1996; Young 2003). Additionally, as the peak in female self-assessment coincides with sexual maturity, this could simply reflect a response to their changing hormonal profile, and assessment of their own reproductive status, which may be adaptive as this is a determinant of eviction likelihood for subordinate females (Young 2003). Further work in this direction is necessary, and a logical extension would be to assess the temporal distribution of self- and intra-group- olfactory assessment, particularly in relation to voluntary dispersal events.

Although kin discrimination has been examined in a number of cases (for a review see Holmes & Sherman 1983), the role of olfaction in this process has rarely been studied (but see Porter et al. 1978; Holmes 1986). The aim of this preliminary study was not to assess the mechanisms of olfactory discrimination, but to make a preliminary investigation into the olfactory discriminatory ability of meerkats in a natural and meaningful ecological context. Although meerkats did not seem to discriminate faeces on the basis of kinship, a larger sample size and the presentation of faeces (and glandular secretions) in a greater variety of contexts would shed additional light on this question.

5

General discussion

The role of latrines in territorial defence is widely accepted, but at present very little is known about individual participation at these sites. Conclusions regarding function are typically based on spatial distribution alone, and as these data are often gathered remotely and without detailed knowledge of the social status of participants, valid conclusions remain limited. In common with other forms of cooperative behaviour, selection is expected to direct participation towards a selfish optimum, with each individual's contribution varying according to the specific costs and benefits it occurs in doing so. Although true for all species, such differences are likely to be particularly profound for cooperative breeders, where the costs and benefits of intruder deterrence are multi-dimensional and vary according to breeding status in addition to sex. Only an integrated approach where all aspects of latrine-use are considered will allow a thorough understanding of this widespread and significant behaviour.

The main aim of this study was to investigate the function of latrine-use in a cooperatively breeding territorial carnivore. Particular attention was paid to the hypothesis that latrines are involved in mate-defence, as this is often a function inferred from general patterns of latrine-use, but one which has received little attention in its own right. This work was divided into three general areas:

1. Where and when do meerkats use latrines?
2. What do particular individuals do at latrines?
3. What information do latrines contain?

This chapter begins with a summary of the results of this research, and its relevance for our understanding of latrine-use and scent-marking in general. Finally, I acknowledge the limitations of this study and suggest potential future directions for research.

5.1 Latrine distribution

Attempting to demonstrate latrine function based on distribution alone is akin to concluding that any written sign hung on a perimeter fence contains a 'private property' message. Although conclusions regarding latrine function based on spatial data alone are not possible, the distribution of latrines can provide valuable information on intended recipients, and direct further detailed work. The results presented here (Chapter 2) provide evidence that meerkat latrines not only facilitate communication between neighbouring groups, but are also distributed in a way that maximises the likelihood of their discovery by transient groups and prospecting males. Firstly, each group shared at least (and usually) one latrine with each known neighbour, which probably facilitates long-term, economical inter-group monitoring. Secondly, the chance of intruders missing widely spaced boundary scent-marks has favoured the adoption of a core-marking strategy (Gorman 1990). Latrines are more likely to be positioned in the exclusive territory, than in the surrounding home range, where overlaps with neighbouring groups occur, but are no more dense in border or core regions of territories. Although extra-group prospecting males and transient groups may enter occupied territories from any direction, groups (Manser & Bell 2004) and prospecting males (Doolan & Macdonald 1996) travel between refuges in the form of boltholes and burrow systems. Latrines are significantly closer to refuge than stringent controls, which increases the likelihood of discovery by these intruders (Chapter 2). This is similar to other species, where the positioning of latrines and scent-marks on trails may promote detection by intruders (e.g. European beaver, *Castor fiber,* Rosell et al. 1998; grey wolf, Barja et al. 2004).

The temporal distribution of latrine-use described here suggests that mate-defence is an important role of latrines (Chapter 2). Groups were significantly more likely to use latrines on days when prospectors were encountered, and tended to do so when females were in oestrus. However, in contrast to a number of other species, meerkat latrine-use is greatest in the period of reduced breeding. An important and similar exception to this general pattern is found in another cooperative breeding carnivore, the Ethiopian wolf, and although intuitively these temporal patterns of scent-marking suggest that mate-defence is not important (Sillero-Zubiri & Macdonald 1998), this is not necessary the case. In other species where dispersal does not coincide with the mating season, scent-marking is significantly higher during the dispersal period (ring-tailed lemur, *Lemur catta,* Gould & Overdorff 2002; sifaka, *Propithecus edwardsi*, Pochran et al. 2005). As peak-dispersal and takeovers occur at this time, latrines may contribute to a long-term mate-defence strategy by assisting dominance retention and increasing future reproductive success. Rather than contradicting the studies on European badgers (Roper et al. 1993) and water voles (Woodroffe & Lawton 1990) where latrine-use peaks in the breeding season, the findings presented here provide additional support for the hypothesis that latrines are involved in mate-defence (Roper et al. 1986).

5.2 Individual behaviour and motivation at latrines

That latrines serve to defend territories *per se* is often assumed, but if this were the case one would expect equal investment on the part of males and females at such sites. However, in the few species where latrine-use has been observed in detail (exemplified by work on the European badger), males scent-marked at elevated rates, concentrated their scent-marking within the breeding season and did so preferentially at boundary latrines (Roper et al. 1993). The mate-defence hypothesis was formulated to explain such patterns (Roper et al. 1986), but despite an increasing number of studies investigating this idea, many of these do not account for the strong possibility that members differing in sex or even dominance status may have different motivations for visiting latrine sites.

The results presented here (Chapter 3) support the idea that ultimate explanations for latrine-use differ according to individual costs and benefits. Meerkats exhibited sex-biased scent-marking at latrines, with males scent-marking at significantly higher rates than females, which is consistent with previously described scent-marking patterns in most species (for a review see Ralls 1971). These results further support a mate-defence function for male latrine-use, as males preferentially over-marked female faeces, and sometimes manipulated experimental latrines to produce male-biased sites. Females scent-marked at significantly lower rates than males but invested heavily in scent-mark investigation, and spent significantly longer sniffing female scent-marks than male scent-marks. As most female terrestrial mammals transmit information about reproductive condition chemically (e.g. Converse et al. 1995), and female reproductive status profoundly affects the life history of other meerkat individuals in the group (e.g. Young 2003), these results suggest that intra-group monitoring of reproductive status is an important function of latrine visits for females. This work is the first direct evidence that, rather than contributing cooperative to territorial defence, individuals selfishly participate in latrine-use only when the benefits accrued outweigh the costs of doing so.

5.3 The information content of latrines

Although latrine location can indicate the intended recipient, and the behaviour of participants may provide further clues as to latrine function, latrine information content and the response it produces in recipients are also important aspects to consider. Although a number of laboratory studies have contributed to our knowledge of the olfactory discriminatory ability of various species, whether and how this information is used in the field has been poorly studied. Well-controlled manipulation experiments are required to support the hypothesis that animals actually use their odour discrimination abilities in social functions (Clapperton et al. 1988).

Prospecting males are more likely to get closer to females, and take-over a group when the number of prospecting males exceeds that of resident males (Young 2003), and so an assessment of group composition would provide useful information. However, the results presented here (Chapter 3) show that as a result of the male dominated scent-marking and preferential over-marking of female scents, the final scent-mark composition of latrines was almost always male-biased, and did not reflect group composition. However, if males were able to discriminate between faeces and scent-marks on the basis of sex, as differential investigation and over-marking patterns suggest (Gsell 2002; Chapter 3), individuals would at least be able to determine the presence of males by assessing these sites.

As latrines are involved in mate-defence, olfactory assessment of factors affecting mating decisions might be expected. Although recipients were more likely to give recruitment calls in response to foreign faeces than to faeces from their own group, olfactory discrimination does not appear to occur on the basis of kinship (Chapter 4).

This is surprising as the deleterious effects of close inbreeding are well known, and regular dispersal in both sexes combined with long dominance tenure result in unfamiliar siblings having a high probability of encountering one another post-dispersal. Although meerkats do not provide help on the basis of relatedness (Clutton-Brock et al. 2001a), it is surprising that meerkats did not discriminate scents on this basis as this would have important implications in mate choice. However, in common with other studies that rely on behavioural responses to bioassays, it is not possible to eliminate the possibility that the recipients perceive but do not respond to differences in scents. Mate-choice decisions are made extra-territorially, and so although one might expect differential response in that setting, foreign individuals on the natal territory may pose a similar threat and so illicit comparable responses in the tested context.

5.4 Limitations and areas of further investigation

The major limitation of this study is that chemical data were not available. Although this was not critical to the questions asked, it would have helped to direct future questions by identifying parameter-specific compounds that would allow me to assess discriminatory ability. Many studies have tackled either the chemical or behavioural aspects of olfactory communication, but few have done both well. Future field studies that take an increasingly integrated approach should produce the most interesting results.

Regarding methodology, although this study assessed the discriminatory ability of meerkats by sequential presentation of the different stimuli, the habituation-discrimination paradigm described by Halpin (1980, 1986) was initially favoured due to its widespread use in laboratory studies. In the field environment however, meerkats habituated quickly to the presentation protocol rather to particular faeces, as individuals did not even investigate samples after one or two prior presentations. Unfortunately, the availability of appropriate samples was limiting, otherwise this protocol could have been extended over a few days. Such an approach is suggested for more long-term studies. Additionally, in any presentation experiments, it would be useful to understand the effects of freezing and sample storage on the specific compounds of interest. Lynch et al. (2003) drew recent attention to the possibility that storage duration and conditions may affect the chemical composition of faeces. In their study, steroid levels in faeces from baboons, *Papio cynocephalus*, varied under different short-term (a few weeks) storage protocols, but usually did so consistently so that determination of pregnancy status was not compromised. This is something that may affect the results of presentation experiments, and should be considered.

A major area that warrants further attention is the response of intruding recipients to latrines of varying composition, and presented in different locations. Females do contribute to latrine sites, although at lower rates than males (Chapter 3), and without assessing the behavioural response of intruders, it cannot be discounted that scents from males and females stimulate differential behavioural responses in recipients. For example, while male scent-marks may signal a commitment to defend females (e.g. Roper et al. 1986), female scent-marks may intentionally advertise their reproductive status to potential suitors. The behavioural effects that latrines of different composition have on intruders are crucial to our understanding of sex- and dominance-differences in scent-marking at these sites, and would add significant weight to functional interpretations of latrines based solely on the distribution and the behaviour of known individuals at these sites. For example, the response of potential prospectors to shared latrines of manipulated scent-mark composition would be a particularly exciting extension of this study. If prospecting could be induced or discouraged according to the relative sex ratio of scent-marks at latrines, this would add further support to the mate-defence hypothesis for latrine-use.

In this study, although I have conducted the most detailed analysis of individual behaviour at latrine sites in any species to date, data from different latrine types were considered together. It would also be interesting to investigate the relative contribution of individuals (particularly males and females) at shared latrine sites against, for example, latrines induced by the presence of prospecting males. As latrines of different types may serve different functions, so it might be expected that individuals adjust their contributions depending on latrine type and location.

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