Scent-marking investment is determined by sex and breeding status in meerkats

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Meerkats, *Suricata suricatta*, engage in cooperative territorial defence, including olfactory demarcation with latrines. Males from neighbouring groups frequently approach resident groups, but, due to high levels of reproductive skew, the potential fitness costs and benefits of deterring these males vary according to the sex and breeding status of residents. Although all individuals visited latrines for similar durations, latrine scent mark composition was highly male-biased. Male behaviour supported a mate-defence function as males scent marked at significantly higher rates than females and preferentially overmarked female scent marks. In contrast to males, female competition is most intense within the group, and females invested heavily in scent mark investigation, but did not selectively overmark existing scent marks of either sex. Monitoring of other females, particularly their reproductive status, may therefore be an important function of latrine visits for females. Rather than cooperatively contributing to territorial defence, individuals appear to participate selfishly at latrine sites, with ultimate explanations for scent marking potentially being related to both the sex and breeding status of group members.

Most social carnivores defend permanent territories against conspecifics (e.g. meerkats, *S. suricatta*: Doolan & Macdonald 1996; spotted hyaenas, *Crocuta crocuta*: Kruuk 1972; European badgers: *Meles meles*: Kruuk 1978). Although traditional explanations suggest that territory owners defend the minimum area necessary to supply them with food (e.g. Davies 1980; Gittleman & Harvey 1982), carnivore territory size is often uncorrelated with group size (Macdonald 1983), which raises the question as to whether territoriality in these species is related to the defence of resources other than food (reviewed in Maher & Lott 2000). In social species where reproduction is unevenly shared, ultimate explanations for territory defence may differ not only between the sexes (e.g. African lions, *Panthera leo*: Packer et al. 1990; Grinnell et al. 1995; Heinsohn & Packer 1995; Pusey & Packer 1997; spotted hyaenas: Boydston et al. 2001), but also more generally between individuals that may benefit differentially

by excluding intruders. These differential costs and benefits will be most extreme when a particular intruder is a reproductive rival to a particular group member, but a potential mate to another.

Many species use communal sites for defecation, and the role of these latrines in territory defence is widely accepted with individuals often depositing glandular secretions along with faeces and urine (Macdonald 1980; Brown & Macdonald 1985). In common with other forms of territoriality (e.g. Pusey & Packer 1997; Boydston et al. 2001), behaviour within the latrine site should approximate the optimal investment for individual participants. 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 sex and seasonal differences in latrine use by European badgers (Neal 1977; Kruuk 1978; Roper et al. 1986, 1993; Brown et al. 1992). These authors suggested that secondary scent marking, which involves placing a scent mark directly on top of an existing mark ('overmarking', Johnston et al. 1994, 1995; Ferkin 1999a, b) or depositing many marks in its vicinity ('countermarking', Hurst 1987),

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might allow resident males to disguise the presence of fe-males on the territory (Roper et al. 1986). More recently, experimental evidence from golden hamsters, *Mesocricetus auratus*, showed that individuals remembered the top, and not the bottom, scent when two scents were only partially overlapping (Johnston et al. 1995) and, in addition to pygmy lorises, *Nycticebus pygmaeus* (Fisher et al. 2003), and female meadow voles, *Microtus pennsylvanicus*, female golden hamsters subsequently preferred to associate with the male whose scent was on top (Johnston et al. 1997a, b). Additionally, female meadow voles preferred to associate with male scent after being experimentally presented with a greater number of overmarks (in different loca-tions) from this male compared to a second male that pro-duced fewer overmarks (Ferkin et al. 2005). This supports the notion that both the frequency of marking (Gosling 1982) and the placement of secondary marks may provide information on the competitive ability or attractiveness of an individual (Rich & Hurst 1999; Ferkin 1999a). Despite this, few field studies have investigated individual invest-ment in scent marking in detail (but see Stewart et al. 2002; Heymann 1998), focusing instead on broad patterns in relation to season. Importantly, very little is known about the relative scent-marking investment of males and females of different breeding status, although the costs and benefits of signalling are likely to vary dramati-cally across these categories and in different contexts. The main aim of this paper therefore is to investigate individ-ual behaviour at latrine sites and, using the cooperative breeding meerkat as a model species, to determine how in-vestment in scent marking and secondary scent marking is affected by the potential benefits accrued by participants.

Meerkats live in groups of up to 49 individuals (T. H. Clutton-Brock, unpublished data). The dominant pair almost monopolize breeding resulting in high reproduc-tive skew, and offspring of both sexes remain in the natal group beyond sexual maturity and assist in raising further litters (Doolan & Macdonald 1997; Clutton-Brock et al. 1998a, 2001; Griffin et al. 2003). While subordinate philopatric males never sire offspring in their own group (Griffin et al. 2003), they do engage in extraterritorial pro-specting forays from about one year of age (Doolan & Macdonald 1996; Young et al. 2005). Subordinate males gain extra-group paternity during these forays (Griffin et al. 2003), and may successfully immigrate into groups by displacing resident males (Doolan & Macdonald 1996; Young 2003). In contrast, female reproductive com-petition is most intense within the group (Clutton-Brock et al. 2006), and dominant females behaviourally suppress the reproduction of subordinate females by expelling them from the group in the latter stages of (the domi-nant's) pregnancy and by infanticide (Clutton-Brock et al. 1998a, 2001; O'Riain et al. 2000; Young & Clutton-Brock 2006). When evicted, females are less likely to con-ceive and suffer an increased likelihood of abortion (Young 2003). None the less, subordinate females may oc-casionally breed in their own group (Griffin et al. 2003; Young & Clutton-Brock 2006), and may obtain dominant status either upon the death of the established dominant, or by forming a new group with unrelated males encoun-tered during eviction (Young 2003).

Meerkat groups visit latrines at significantly higher rates during the peak breeding period in general, and also when extra-group males approach, suggesting that latrines are involved in mate defence and signalling to male intruders in this species (Jordan et al. 2007). As a result of differen-tial access to reproductive partners, sex- and status-biased investment in intruder deterrence might be expected, as the benefits of deterring extra-group males differ dramati-cally between individuals. While resident male meerkats may increase their direct fitness via mate-defence strate-gies, females may benefit from encounters with extra-group males through increased mate choice and mating opportunities.

To address these questions I collected detailed behav-ioural observations to quantify individual investment at latrine sites. First, I assessed whether latrine composition reflects group composition such that demographic in-formation might be obtained by intruding males during latrine visits. Second, I investigated the factors affecting scent mark investigation and overmarking patterns at naturally occurring latrine sites. Finally, I conducted pre-liminary experimental presentations using latrines of controlled composition in an attempt to assess whether individuals might bias the composition of these sites through selective overmarking.

METHODS

Study Area and Population

Data from 38 latrine visits from 11 groups were collected between June and December 2004, representing 3.46 ± 0.55 ($\overline{X} \pm$ SE) visits per group (range $1-6$). The study site encom-passed the Kuruman River Reserve and surrounding ranch-land in the southern Kalahari ($28°58'$S, $21°49'$E), and is bisected by the dry bed of the Kuruman River, consisting of sand dune, river terrace and river bed habitats (for further details see Clutton-Brock et al. 1999 and Russell et al. 2002). The study was carried out under a permit issued by the Northern Cape Conservation Service, South Africa. Groups ranged in size from 6 to 25 individuals, and were habituated to close human observation (<1 m) and handling. To allow rapid individual field identification, unique (ca. $1-1.5$ cm^2) hair-dye marks were applied to each individual's pelage while they sunned themselves in the mornings, and these were renewed every few weeks. Additionally, one individual in each group was fitted with a radiocollar (Sirtrack Havelock North, New Zealand), and some individuals remained col-lared at the end of the study period as the long-term project continued. Details of capture, collaring and marking proce-dures are described elsewhere (Jordan et al. 2007). Groups were visited at least every 3 days during the study to assess group composition and to collect behavioural data, and the age of all study individuals was accurately known (usu-ally to the nearest day) as they had been studied since birth. Six categories of individual were included in analyses for this study: subadults ($6-12$ months) and adults (>12 months) were categorized by sex, and adults were further divided ac-cording to their dominance status. The dominant pair was readily recognized from subordinates by their regular

dominance assertion behaviours (Kutsukake & Clutton-Brock 2006).

Data Collection and Definitions

Latrine sites typically contained 5 to >100 faeces in a 0.5–6 m^2 area, and visits almost always included the deposition of other scent mark types, such as *anal* marking and *chew* marking, in addition to further *faecal* or *urine* marking. Anal marking involves wiping the anal region across a surface, most commonly across vertical surfaces such as trees, bushes or refuge entrances, but also along the ground in an 'anal drag' (Rasa 1973). Chew marking involves biting vegetation, and usually includes rapid head thrashing. As faeces and urine were deposited at latrine sites, their inclusion as scent marks is justified following the criteria of Kleiman (1966) in that they were (1) repeated frequently on the same object or in the same location, (2) elicited by familiar landmarks and novel objects or odours, and (3) often oriented towards specific objects. Additionally, individuals were seen to defecate and urinate on multiple occasions during a single latrine visit. Urine marking was distinguished from simple elimination, as it involved cocking a rear leg and directing the urine onto a vertical surface or an existing scent mark. Meerkats were observed to place all scent mark types over, or at least partially over, all other scent mark types in this study. Additionally, latrines were covered with multiple small pits, which were produced by frenzied digging or 'scuffing'. Faeces were scattered individually in and around pits, and more rarely 2–6 faeces were deposited in a single pit.

Video recordings were made of each latrine visit using either a Sony CCD-TRV46E analogue or DCR-PC120E digital camcorder from a Starfoto tripod set 52 cm above ground level. Recordings were viewed for analysis using Microsoft Windows Media Player (XP version) on a 15-inch monitor. The field of view was set to incorporate the entire latrine site (typically covering about 8 m^2), and the total time that individuals were in the latrine was recorded as the time spent within the field of view. 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.

All individuals were followed using focal-animal sampling from the video recordings (Altmann 1974). The proportion of total time that individuals were engaged in: (1) scent mark investigation, (2) vigilance, (3) scent marking and (4) scuffing were calculated. Individuals were considered vigilant when they were bipedal; quadrupedal individuals were considered vigilant when they were immobile with the head raised above ground and were not engaged in any other activity. All instances of scent marking were recorded by continuous sampling (Martin & Bateson 1993), 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 with a permanent marker pen. Although Johnston et al. (1994) distinguish between over- and countermarking depending on whether subsequent marks completely or partially overlap the previous mark, respectively, subsequent work from the same laboratory and others suggest that scent blending does not occur, as only the top mark is perceived and 'remembered' later (e.g. Johnston et al. 1995). I therefore define overmarking as the deposition of scent marks either partially or completely onto existing scent stations, and include situations where a scent mark was placed on the location of another faeces if it was preceded by scuffing which resulted in the total burying of the existing faeces. Changes in scent station composition throughout the latrine visit (by the addition of subsequent marks) were recorded, and so scent station composition at any point of time was known. For each scent mark, the mark type, the markers identity, the time of deposition and the scent station number were recorded. A 'top mark' was the most recent scent mark placed on a scent station, and by necessity it was assumed that each latrine contained no scent marks at the onset of each visit by a group. Scent signals are unlikely to persist over typical latrine visit intervals, as the majority (20) of latrines in this study were singly used latrines (sensu Jordan et al. 2007) that were not observed to be visited at all in at least 12 months prior to collection of the data reported here. Although at least one prior visit to the remaining 18 latrines was observed, the most recent recorded visit occurred 95 ± 77 ($\overline{X} \pm SD$) days (range 11–283) prior to data collection. Although this figure probably overestimates intervisit intervals (as it was not possible to continuously follow all groups simultaneously), the mean actual interval is unlikely to be less than about 1 month, as groups were followed by other observers for about one-third of their active period.

Scent Mark Investigation and Overmarking Patterns

Individual investigation duration was recorded to the nearest second. Only overmarking events preceded by investigation of the original mark were included in analyses of overmarking to remove 'random' overmarking from analyses. Factors potentially affecting scent mark investigation or overmarking included: scent mark type; the age, dominance status, sex and relative sex (relative to the recipient) of the depositing individual; and the number of marks, and age, sex, relative sex and dominance category of the individual that deposited the top mark. In all comparisons, scent stations were similar to each other except for the factor under investigation. All analyses involved paired data on the responses of a given individual to comparable scent marks during the same latrine visit; only responses to the first encountered scent marks of each specified composition were compared.

Own-mark investigation and reinforcement marking (where an individual overmarks a station where its own mark is already the top mark) were not included in analyses, as sequential multiple marking on the same spot may occur as a frenzied response to the first stimulus.

Eliminative (faeces and urine) and noneliminative scent marks were considered separately. Scent stations containing eliminative marks were not incorporated into analyses involving the response of individuals to scent stations already containing multiple scent marks, as I could not justify assigning them equal weighting with glandular secretions.

Presentation Experiment and Sample Storage

Six dominant females and six dominant males were presented with a unique artificial latrine containing 4 faeces from their own group, randomly positioned in a line on a sand-covered tray with interfaeces distances of 8 cm. In each case samples were from dominant and subordinate adults of each sex. The tray was placed 0.5−1 m away from the foraging individual, and responses were recorded on video at a distance of 1.5−3.5 m. If a nontarget 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 and transferred to individual zip-lock bags using a small plastic spoon, which was cleaned between sample collections. Samples were placed on ice and stored in a freezer (-2 to $-6°C$) within 4 h. Samples remained frozen for 7.83 ± 1.43 ($\bar{X} \pm$ SE) days, $N = 24$ (range 0−19) before presentation to dominant males, and 7.96 ± 1.28 days, $N = 28$ (range 0−19) to dominant females, and were defrosted simultaneously in the sun for 10 min prior to presentation. Samples were age-matched as far as possible, with the oldest and youngest sample differing by 0 to 8 (3.83 ± 1.17) days for males, and 0 to 10 (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 recipients perceived subtle age differences is not known.

Statistical Analyses

All statistical tests were carried out using Minitab Release 12.21 (Minitab Inc., State College, PA, U.S.A.), or the Analyse-IT extension for Microsoft Excel (Analyse-it Software, Ltd, Leeds, U.K.). I used parametric statistical tests unless the data differed significantly from normal (based on the Anderson−Darling test for normality). In these cases, equivalent nonparametric statistics were used. Proportional data were arcsine square-root transformed to meet the equal variance and normality assumptions of ANOVA and nonproportional data were log transformed where possible. Post hoc tests on activity budget data were carried out following Day & Quinn (1989). 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). Within the scent mark investigation and overmarking analyses, data were 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, and only the first scent marks of each specified composition that each adult individual encountered were included in statistical comparisons. All 32 latrine visits where at least one scent mark was deposited were used in the final composition analysis, and all results are presented as mean $\pm$ SE.

RESULTS

A total of 254 scent stations were identified with 1−19 scent stations per latrine visit (7.94 ± 0.90, $N = 34$). During latrine visits, 60.6% of scent stations were marked only once, 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. In total 635 scent marks were observed, of which most were anal marks ($N = 486$). The frequency and percentage of scent marks of each type are shown in Table 1.

Latrine Composition

In 32 latrine visits where at least one mark was deposited, latrine scent compositions did not correlate with group composition (Fig. 1). Group size was not correlated with 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, neither the proportion of all scent marks that were deposited by males nor the proportion of scent stations with a male top mark were correlated with either the adult sex ratio (All marks: $r_s = -0.028$, $N = 33$, $P = 0.88$; Top marks: $r_s = -0.068$, $N = 33$, $P = 0.71$) or the overall sex ratio of the group (All marks: $r_s = -0.110$, $N = 33$, $P = 0.54$; Top marks: $r_s = -0.028$, $N = 33$, $P = 0.88$). Seventy-one per cent ($N = 27$) 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

Table 1. The frequency and percentage of the four scent mark types deposited during the study period by dominant males (DM), dominant females (DF), subordinate males (SM) and subordinate females (SF)

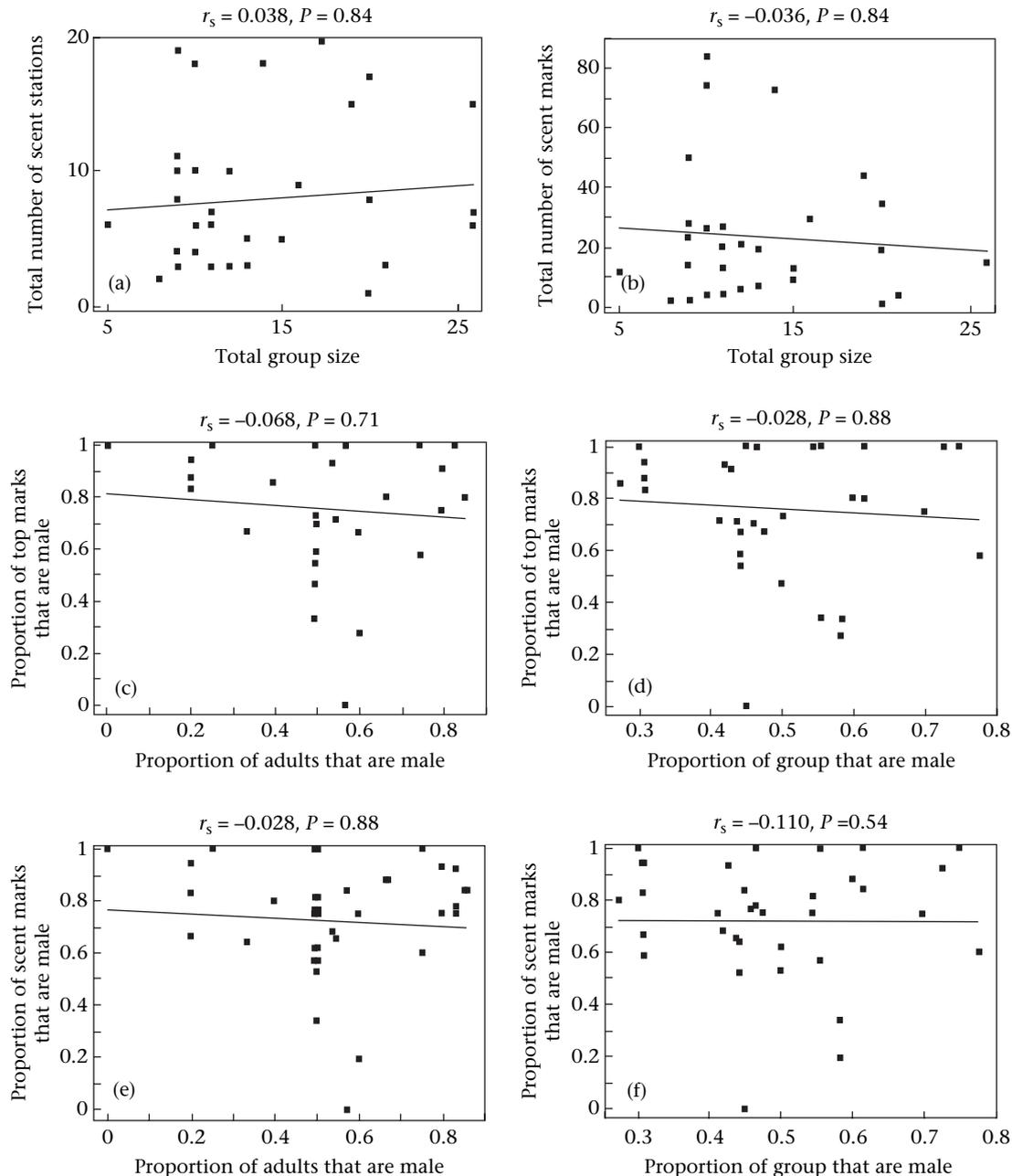|	Anal	Chew	Faeces	Urine
DM	295	47	20	9
	79.5%	12.7%	5.4%	2.4%
DF	127	19	14	3
	77.9%	11.7%	8.6%	1.8%
SM	62	10	22	0
	66.0%	10.6%	23.4%	0%
SF	2	1	4	0
	28.6%	14.3%	57.1%	0%
Total	486	77	60	12
	76.5%	12.1%	9.5%	1.9%

Figure 1. Scatter plots of (a) total group size against the total number of scent stations; (b) total group size against the total number of scent marks; (c) the proportion of adults that are male against the proportion of scent stations with a male top mark; (d) the proportion of the group that are male against the proportion of scent stations with a male top mark; (e) the proportion of adults that are male against the proportion of scent marks made by males; and (f) the proportion of the group that are male against the proportion of scent marks made by males. Shown are lines of best fit, and statistics are for Spearman rank order correlations.

common, the dominant male was either absent from the group or did not enter the latrine, and a third contained only a single female faeces (deposited in an existing latrine site).

Activity Budgets

Different categories of individual did not vary significantly in the total time spent in latrines (ANOVA:

$F_{5,36} = 0.67$, $P = 0.65$) or the proportion of this time spent investigating scent stations or being vigilant (Kruskal–Wallis test: investigation: $H_5 = 6.84$, $P = 0.23$; vigilance: $H_5 = 1.42$, $P = 0.92$; Fig. 2). However, the proportion of time that individuals spent scent marking varied significantly with individual category (ANOVA: $F_{5,52} = 5.71$, $P < 0.001$). 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
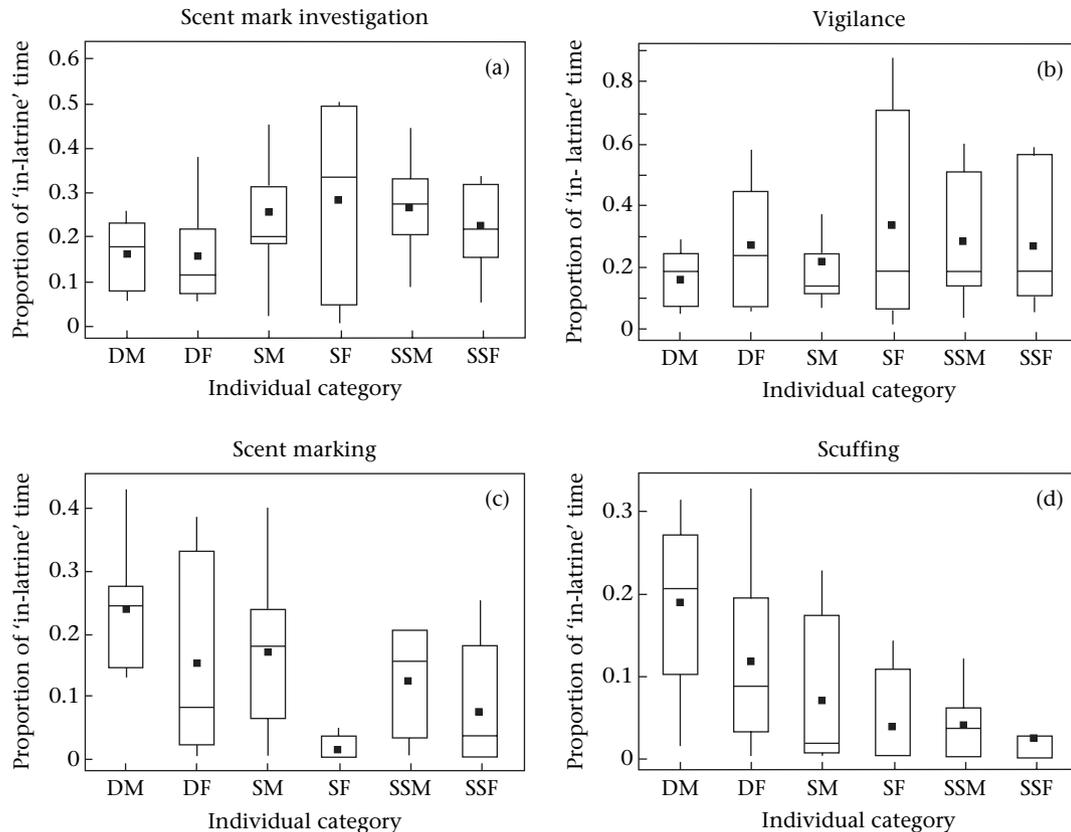
Figure 2. Box plot showing the proportion of total in-latrine time different categories of individual invested in: (a) scent mark investigation; (b) vigilance; (c) scent marking; and (d) scuffing. Solid points are medians, boxes represent interquartile ranges, and vertical lines show the total range of values. DM = dominant males, DF = dominant females, SM = subordinate males, SF = subordinate females, SSM = subordinate subadult males, SSF = subordinate subadult females.

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 any other category of individual, with the exception of subordinate subadult females ($P < 0.05$). The proportion of 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 females of the same age and dominance status (Fisher's pairwise test $P < 0.05$).

Scent Mark Investigation and Overmarking Patterns

Overmarking by adult meerkats was observed on 228 occasions, with 70% of overmarks preceded by investigation (sniffing) of the original mark. Considering single scent marks only, there was no significant difference in time spent investigating faeces from opposite- or same-sex individuals (paired t test: $t_{12} = 1.07$, $P = 0.31$), and individuals spent similar amounts of time investigating female faeces and male faeces ($t_{12} = 0.15$, $P = 0.884$).

Overmarking of faeces showed a sex bias in males, but not in females, with 75% ($N = 16$) of all faecal overmarking 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 overmark the faeces of an adult female than the faeces of an adult male (Fisher's exact test: $N = 26$, $P = 0.04$), but females were no more likely to overmark the faeces of males or females ($N = 20$, $P = 0.39$).

On noneliminative scent stations, males were significantly more likely to overmark those with a female top mark than scent stations with a male top mark (Fisher's exact test: $N = 26$, $P < 0.01$), overmarking scent stations with female top marks on 86.7% of encounters compared to only 23.3% for scent stations with male top marks. On the few occasions when females encountered a noneliminative scent station with a (nonself) female top mark, only 16.7% were overmarked ($N = 6$), compared to scent stations with male top marks which were overmarked on 46% of encounters ($N = 50$). Females overmarked 41% of (17) encountered female scent marks or scent stations with (nonself) female top marks compared to 48% of (69) male marks or top marked scent stations. 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 scent station of each category during a single latrine visit (Kruskal−Wallis test: $H_2 = 2.30$, $P = 0.32$).

It was not possible to statistically compare differences in investigation and overmarking patterns for single non-eliminative scent marks of differing sex, as encounters with single noneliminative scent marks from females were extremely rare. However, dominant males overmarked all opposite sex single noneliminative scent marks encountered ($N = 5$) compared to only 50% ($N = 4$) of scent marks from the same sex. Only one female scent mark was encountered by a dominant female during the study, and this was not overmarked, but dominant females overmarked 56% ($N = 9$) of encountered male scent marks.

Experimental Presentations

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, while 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 (Fig. 3) but sample size did not allow statistical comparison.
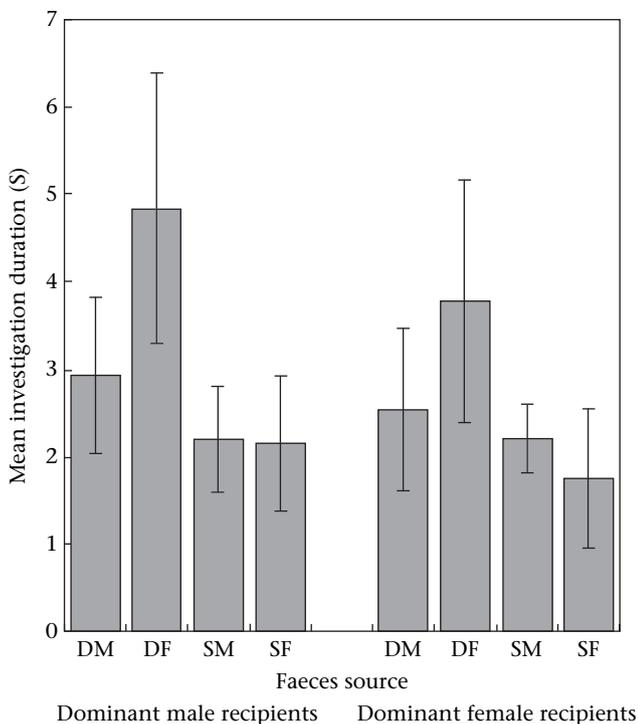

Figure 3. Investigation duration (s) for faecal samples from dominant males (DM), dominant females (DF) subordinate males (SM), and subordinate females (SF), during latrine presentations to dominant males (left) and dominant females (right). Error bars represent standard errors.

DISCUSSION

In common with many other species (e.g. Eurasian beaver, *Castor fiber*: Rosell & Thomsen 2006), meerkat scent-marking behaviour was sexually dimorphic. Although dominant and subordinate adults of each sex spent similar amounts of time in latrines, males invested significantly more time scent marking, while females were primarily engaged in investigating scent marks. As the most common intruders into meerkat territories are extra-group males, this fits previous descriptions of territorial behaviour in general (e.g. African lions: Packer et al. 1990; Grinnell et al. 1995; Heinsohn & Packer 1995), where heightened responses to intruders of the same sex are common in many species (e.g. banded mongooses, *Mungos mungo*: Cant et al. 2002; spotted hyaenas: Boydston et al. 2001). However, due to the skew in reproductive opportunities within groups, the potential fitness costs and benefits of signalling to intruders also vary within each sex according to breeding opportunities, and scent-marking patterns seem to reflect these potential costs and benefits.

Patterns of scent marking by male meerkats support a mate-defence function. Males were significantly more likely to overmark female faeces and scent stations with female top marks, whereas females showed no preference, resulting in the vast majority of scent stations in each latrine having male top marks. These results are interesting in light of the recent finding that female meadow voles are able to 'count' overmarks, and subsequently prefer to associate with the odours of males whose marks were experimentally placed as overmarks at greater frequencies (Ferkin et al. 2005). Although some authors have argued that if scent marks serve to advertise an individual's presence in an area then individuals should avoid marking locations previously marked by others (e.g. Thomas & Wolff 2002), previous experimental work has shown that individuals presented with partially overlapping scent marks subsequently remembered only the top mark (golden hamsters: Johnston et al. 1995), or seemed to assign more value to it (prairie voles, *Microtus ochrogaster*: Woodward et al. 2000). Although all reported overmarking experiments involved only intrasexual overmarking, it is possible that male scent marks placed over the existing marks of females may mask the presence of these female marks. Selective overmarking of female marks by male meerkats may therefore disguise the presence of resident females, or advertise a commitment to defend them, as first suggested for European badgers (Roper et al. 1986). In addition to previous work showing that meerkat groups visit latrines at higher rates in the breeding season and in response to intruding males (Jordan et al. 2007), such male-biased marking rates and overmarking supports a mate-defence strategy.

If mate defence is an important factor explaining male scent-marking investment, nonbreeding subordinate males might be expected to scent mark at lower rates than (breeding) dominants, as is common in many mammals (e.g. Ethiopian wolves, *Canis simensis*: Sillero-Zubiri & Macdonald 1998; coyotes, *Canis latrans*: Gese & Ruff 1997; ring-tailed lemur, *Lemur catta*: Kappeler 1990).

Instead, subordinate males scent marked at similar (although slightly lower) rates as dominant males but at significantly higher rates than females. Although this superficially appears to contradict the mate-defence hypothesis, natal subordinate male meerkats may increase their inclusive fitness by deterring foreign males. Subordinates of both sexes provide costly care to the dominants offspring mainly in the form of babysitting (Clutton-Brock et al. 1998a, 2000) and pup provisioning (Clutton-Brock et al. 2001), and although contributions to cooperation are not kin-biased in meerkats (Clutton-Brock et al. 2001), strategies which increase the relatedness of pups to helpers would maximize the inclusive fitness gains of helping. By assisting their father in mate defence, subordinate sons could increase their relatedness to offspring that they assist to rear.

Intense intragroup reproductive conflict between female meerkats may explain why females spent significantly longer investigating scent marks than males did. Although small sample size did not allow statistical comparison, recipients of experimental latrines also investigated the scent marks of dominant females for longer than the scent marks of other individuals. This strongly suggests that meerkat scent marks are sex-specific, as has been shown for a number of species (e.g. Siberian weasel, *Mustela sibirica* and Steppe polecat, *Mustela eversmanni*: Zhang et al. 2002), but scent marks of a number of mammals also vary with reproductive status (e.g. greater galalgos, *Galago crassicaudatus*: Clark 1982), and the ability to discriminate between scents on the basis of reproductive status appears to be common (e.g. giant pandas, *Ailuropoda melanoleuca*: Swaisgood et al. 2002; pygmy marmosets, *Cebuella pygmaea*: Converse et al. 1995). Although acquisition of such information would benefit all group members, females are most profoundly affected by the reproductive status of other females. Subordinate females are expelled from the group in the latter stage of the dominant's pregnancy (Clutton-Brock et al. 1998b). As dominant females are more likely to evict pregnant subordinates (Young 2003), probably because pregnant females pose an infanticide risk (Clutton-Brock et al. 2001; Young & Clutton-Brock 2006), subordinate females that conceal their pregnancy status by defecating and urinating away from latrine sites may potentially delay expulsion. Indeed, subordinate females scent marked significantly less in latrines than other individuals. In many callitrichid cooperatively breeding primates, dominant female scent marks are involved in the suppression of subordinate ovulation (e.g. cotton-top tamarins, *Saguinus oedipus oedipus*: Savage et al. 1988; common marmosets: Barrett et al. 1993) but whether this is also true for meerkats remains unknown.

Dominant females scent marked at significantly higher rates than subordinate females. Although dominant females may benefit from the presence of extragroup males through increased mate choice, the presence of these males also increase female reproductive conflict by providing subordinate females with mating opportunities. Given that pregnant subordinate females pose a risk to the dominant's young (Young & Clutton-Brock 2006), denying subordinates access to extra-group males may be yet another counterstrategy that dominant females use to monopolize reproduction.

In summary, strategies for maximizing reproductive success differ between the sexes (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 prospecting males has differential costs on group members according to their sex and status within the group, latrine behaviour may be better explained as serving selfish interests rather than cooperative defence. Whereas male meerkat behaviour fits the hypothesis that latrine use and scent marking are involved in mate defence, lower scent-marking investment and nonselective overmarking by females suggest that they do not visit latrines to signal to extra-group males. Instead, females may benefit from latrine visits by assessing the reproductive status of other individuals within the group, which has a profound effect on their own survival and reproductive success. Further experiments are necessary to determine the responses of prospecting males to scent marks of each sex and to latrines of mixed composition.

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