Ethology

Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew

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Abstract

Most mammals scent-mark and a variety of hypotheses have been put forward to explain this behaviour. Differences in the main function of scent-marking between species are likely to be related to differences in social systems. Here, we investigate the functions of scent-marking in a cooperatively breeding carnivore. In the banded mongoose (*Mungos mungo*), individuals of both sexes commonly breed in their natal group and reproductive skew within groups is low. Using experimental scent-mark presentations, we tested predictions of the intrasexual competition, self-advertisement to potential mates and dominance assertion hypotheses. Both males and females responded more intensely to scent marks of same-sexed than of opposite-sexed individuals. Dominant individuals counter-marked more than subordinate ones and males showed higher counter-marking rates than females, but only marginally so. During oestrus, responses to scent marks were increased by both sexes. Our findings strongly indicate that scent-marking in the banded mongoose primarily serves a purpose in intrasexual competition both between and within groups. Unlike in other social herpestids and some solitary rodents, we found little evidence for self-advertisement. We suggest that the peculiar social system of the banded mongoose results in self-advertisement losing importance in this species, shifting the main function of scent-marking to intrasexual competition.

Introduction

Most mammals scent-mark, with urine, faeces and/or secretions of scent glands (Ralls 1971; Thiessen & Rice 1976). The main function of scent-marking was long thought to be territory defence (Hediger 1949; Gosling 1982; Gorman 1990). However, in a number of species the territory defence hypothesis is not supported by empirical data and some non-territorial species also scent-mark (Ralls 1971; Johnson 1973; Heymann 2006). Scent marks probably mediate individual and group recognition in most species (Ralls 1971; Johnson 1973; Gosling & Roberts 2001), whereas in only few species labelling of the home range is thought to be an important function of scent-marking (e.g. black rhinoceros: Goddard 1967; slow loris: Seitz 1969; klipspringer: Roberts 1997). Evidence for the orientation hypothesis is mostly indicative or it is accepted as default after rejecting other hypotheses (Brashares & Arcese 1999).

Several other, not mutually exclusive functions have been proposed, including intrasexual competition, self-advertisement to attract mates and dominance assertion (reviewed in Ralls 1971; Johnson 1973; Gosling & Roberts 2001). Support for the intrasexual competition and self-advertisement hypotheses has accumulated particularly in primates (reviewed in Heymann 2006), rodents (Rich & Hurst 1999; Thomas & Wolff 2002; Wolff et al. 2002) and herpestids (Wenhold & Rasa 1994; Jordan 2007). The dominance assertion hypothesis applies in particular to social species but is difficult to disentangle from the intrasexual competition hypothesis as dominance and competition over reproduction are often tightly linked (Drews 1993; Heymann 2006).

The main function of scent-marking in a given species is probably related to its social system. In solitary species, territory defence and self-advertisement to attract mates may be more important than intrasexual competition for breeding opportunities. In social species, dispersal differences are probably linked to different roles of scent-marking. Individuals that leave the natal group to breed elsewhere, in mammals that is typically the males (Greenwood 1980), probably profit from self-advertisement to potential mates, but do not compete with same-sexed residents of their natal group. In contrast, philopatric individuals may have no need to attract mates but rather to secure their breeding position against same-sexed competitors. Here, we investigate the functions of scent-marking in the banded mongoose (*Mungos mungo*), a small, cooperatively breeding carnivore which is particularly interesting in this context because both sexes regularly breed in their natal group (Cant 1998; Gilchrist 2001) and reproductive skew is low (Cant 2000).

Banded mongooses, like other herpestids, scent-mark using faeces, urine and secretions of scent glands (Brown & MacDonald 1985; Müller & Manser 2007). In banded mongooses as well as in the closely related meerkats (*Suricata suricatta*), the spatial distribution of scent marks suggests that territory defence is not the primary function of this behaviour (Jordan et al. 2007; N. R. Jordan pers. comm.). The density of scent marks is higher in the core areas of the home ranges, which matches the higher utilization of these areas. That is, the distribution of scent marks is consistent with random spatial distribution in this species. However, conspicuous marking spots shared between neighbouring groups indicate that marking may still play a role in territory demarcation. More likely, scent-marking is heavily involved in communication within and between groups. Banded mongooses not only recognize scent marks of their own group, but also differentiate between scent marks of different neighbouring groups and strangers (Müller & Manser 2007). Because of the intense competition for reproduction (Cant 2000; Cant et al. 2001, 2002; Gilchrist 2006a), scent-marking is probably involved in intrasexual competition and possibly in self-advertisement in this species.

Within banded mongoose groups, reproductive skew is generally low, with all mature females breeding regularly and commonly in synchrony (Cant 2000). Nevertheless, there is intense intrasexual competition for breeding opportunities among females, indicating that the costs of reproductive suppression outweigh the benefits to dominants in this species (Clutton-Brock 1998; Gilchrist 2006b). In large groups in particular, subordinate females may get temporarily or permanently evicted from the natal group during oestrus or pregnancy and thus prevented from breeding or forced to abort (Cant et al. 2001; Gilchrist 2006a). Only a small proportion of all breeding attempts involve eviction (Gilchrist 2006a) and the factors triggering an eviction event are still largely unknown. Competition among females is likely not for access to males but rather for helpers which, in this cooperatively breeding species, are crucial for the successful rearing of offspring (Cant 2003; Gilchrist 2004; Hodge 2005).

Males also compete for breeding opportunities. During oestrus, females are mate guarded by dominant males, which restricts breeding opportunities of subordinate males (Cant 2000). Oestrus of females within groups is commonly synchronized (Cant 2000) and therefore any single male can only guard one to two females per oestrus period. Thus, multiple males are breeding. Also copulations of females with males other than the mate guarding ones occur. It is not known how efficient mate guarding in this species is in securing paternity. However, as banded mongoose groups are commonly heavily male biased (De Luca & Ginsberg 2001), young subordinate males are probably prevented from breeding. Eviction of subordinate males also occurs, but less frequently than for females (Cant et al. 2001; Gilchrist 2001; Hodge 2003; Bell 2006).

Intrasexual competition extends beyond the own group for both sexes. Individuals of either sex may leave the natal group either voluntarily or via eviction by co-residents. These individuals either found new groups or attempt to take over small groups, thereby displacing their same-sexed rivals permanently (Cant et al. 2001; Gilchrist 2001). Females in oestrus may also mate with males of other groups during inter-group interactions and it has been suggested that dominant females, when in oestrus, may actively seek interactions and matings with males of neighbouring groups (Cant et al. 2002). However, contrary to meerkats (Young et al. 2005), banded mongooses of neither sex leave the group temporarily to search for mating opportunities with partners in other groups.

We used a large dataset of experimental scent-mark presentations (Müller & Manser 2007) to test predictions of the intrasexual competition, self-advertisement to mates and dominance assertion hypotheses. The intrasexual competition hypothesis predicts higher rates of scent-marking in the sex with stronger intrasexual competition. As typical for mammals, competition among males is intense in banded mongooses. However, as females also compete for breeding opportunities, sex differences in marking rates are predicted to be small. The intrasexual selection hypothesis further predicts that the response to scent marks of same-sexed individuals is stronger than to those of opposite-sexed individuals and that counter-marks are placed on top of the original marks. Furthermore, scent-marking rates should increase during oestrus. If scent-marking plays a role in self-advertisement, counter-marks should be placed separate from rather than on top of the original marks to maximize individual identity (Thomas & Wolff 2002) and females should increase their marking rate when in oestrus. Also, subordinate individuals should be particularly interested in scent marks of opposite-sexed individuals from other groups and they should increase scent-marking rates in peripheral areas compared with core areas of the groups' home ranges. Finally, the dominance assertion hypothesis predicts that scent-marking is mostly performed by dominant and rarely by subordinate individuals.

Methods

The study was conducted on a wild population of individually marked banded mongooses in Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E) between April 2004 and August 2005 (for details on the study site see Cant 2000). The study population remained largely constant in size throughout this period and consisted of 210–240 individuals in nine groups, seven of which were habituated to close observation and were included in the experiments described below. The size of these seven groups ranged from 8 to 44 individuals. Animals were classified in age classes as adults (>12 mo), subadults (6–12 mo) and infants (<6 mo). Date of birth was known for all individuals except for nine adult immigrants. All animals were trapped on a regular basis to refresh individual marks (colour-coded plastic collars or small shaves on the rump), detect pregnancies, take morphometric measures and estimate ectoparasite load (for details see Cant 2000). For trapping as well as for scent-mark presentations, small amounts of bait were used (a mix of rice and gravy).

We assigned dominance status to adult individuals based on eviction events for females and based on mate guarding behaviour for males (Cant 2000). In three of the seven groups, eviction of females was observed during the study period. This allowed a clear distinction between dominant females (aggressors) and subordinate females (evictees). Aggressors were invariably the two or three most senior females and commonly all younger adult females were evicted. In the groups where no eviction was observed, the two most senior females were considered dominant and females below 2 yr of age were considered subordinate. The remaining females were not assigned to either dominance category. Males which were observed regularly mate guarding dominant females were considered dominant, whereas males were considered subordinate until they started to show mate guarding behaviour (approximately at an age of 2 yr). Males that were occasionally involved in mate guarding were not assigned to either dominance category. Infants and subadults as well as adults that could not be assigned to a status category (12% of the females, 36% of the males) were not included in the analyses of dominance effects.

Scent-Mark Presentations

In separate trials, each group was presented with excreta (faeces and urine) collected from neighbouring groups, non-neighbouring groups (strangers) and the group itself (own group). This setup allowed testing the role of scent-marking in communication both between and within groups. Treatments were performed in two categories of locations (centre and border of the home range).

For each trial, six or seven samples of fresh excreta were collected from the donor group within 1 h. For that purpose, the groups were presented with a clean 2 m^2 plastic sheet that, like any smooth surface, induced the mongooses to defecate and urinate (C. A. Müller, pers. obs.). Faecal samples were collected with a spoon. Urine samples deposited away from the plastic sheet were also collected with a spoon, including the substrate. Urine samples deposited on the sheet were collected with a pipette and later mixed with soil.

The set of scent marks consisted of scat and urine samples from 5 to 7 individuals (4–7 adults and 0–3 subadults and infants) and included samples of adult males and adult females and of both excretion types. Samples were used only in one experiment and then discarded and only samples with known identity of the excreting animal were used. If insufficient samples were collected *ad libitum*, we trapped several individuals and collected excreta from the traps. This procedure represented only minimal stress as all individuals in the study population have been trapped on a regular basis (2–4 times a year, for details see Cant 2000). Trapped animals were released within 15 min of trapping which is well below the delay time between peak of hormones in the blood and in the faeces for mammals (Palme et al. 2005). However, we cannot exclude that faecal samples collected by trapping were more or less likely to include secretions from the anal glands (Asa et al. 1985). Of all samples, <20% were collected by trapping and these were not inspected longer than samples collected *ad libitum* (Müller & Manser 2007).

The collected samples were stored on ice and presented to the experimental group on the same day (on average 2 h after collection). As banded mongooses often use open patches for territorial marking (C. A. Müller, pers. obs.), the samples were arranged in a circle on open ground (spaced apart 30–50 cm). This enabled accurate observation of the mongooses' response from 5–10 m distance. We scattered 20–50 g of bait in a circle at 2–4 m distance to the samples to make sure that the mongooses would find the presented stimuli. The experiments were recorded for later analysis using a digital video camera (Panasonic NV-GX7; Matsushita Electronic Industrial Co. Ltd., Osaka, Japan) and a Sennheiser ME 66/K6 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, USA). Recording was stopped when no individual had approached any of the presented samples for 60 s.

The following response variables were evaluated: (1) duration of inspection bouts; (2) worry calls; and (3) counter-marking. The duration of inspection bouts (one individual inspecting one sample) was determined frame-by-frame in Windows Movie Maker (Microsoft Corp.; 1 frame = 0.08 s). Worry calls are typically given upon encountering secondary cues of other mongooses or predators and are assumed to indicate how unsettling the stimuli were to the inspecting individuals (Müller & Manser 2007). Data on different types of counter-marks were pooled (anal marking: 69% of all marks, urinating: 19%, defecating: 12%). This had several reasons: first, sample sizes for the two rare counter-marking types were too small for separate analysis. Second, we were interested in broad patterns of response intensity rather than specific responses. Finally, different marking types may have different functions (Rasa 1973), but we did not have any *a priori* knowledge on which type is relevant in the investigated context. However, we also conducted the analyses looking only at anal marks. This did not change the outcome, with one exception where this is indicated (Table 2).

In total, we performed 96 experiments with seven subject groups. Sample sizes for the different analyses (summarized in Appendix, Table A) were lower for one or a combination of the following reasons: (1) the duration of single inspection bouts was determined for only 74 of the experiments. For the remaining 22, only worry calls and counter-marks were recorded. (2) Dominance status could not be assigned to all individuals (see above). (3) Not all worry calls and counter-marks could be assigned to an individual sample. (4) The identity and sex of the responding individual could not be determined for all worry calls and counter-marks. Five of the experiments were performed when females of the acceptor group were in oestrus (in total nine individuals) and during five experiments samples collected from females in oestrus were presented (in total nine samples). In some cases, it could not be decided reliably whether a female was in oestrus on the day of the experiment and these data points were excluded from the analyses of oestrus effects.

Statistical Analyses

The duration of single inspection bouts was normalized by log-transformation and analysed in linear mixed models (LMMs) using the restricted maximum likelihood (REML) method and Type I sums of squares. Group identity and individual identity (nested within group) were included as random factors. Additionally to the tested factors (see Appendix, Table B), we controlled for effects of donor category (own group, neighbouring group, strangers) and inspection order (1st, 2nd, etc, sample an individual inspected during a particular experiment). The effects of dominance and donor status were analysed with reduced datasets (see above) and the models included all factors found significant in the analysis outlined above. The effect of oestrus on inspection was analysed as described above with the exception that the dataset was restricted to female samples (donor group in oestrus) or split by sex (acceptor group in oestrus) and excluded infants as they were not sexually mature. All p-values reported are of the respective factor entered last in the model. Non-significant interaction terms were not included in the models. However, interaction terms that were used to test specific predictions are reported also if non-significant.

The frequencies of worry calls and counter-marks were analysed with chi-square tests comparing observed and expected frequencies which were based on the number of individuals in each class which had inspected the presented samples. For the analysis of sex-specific responses to scent marks, expected values were based on the number of male and female samples that were presented. Over all experiments, on average 4.2 male and 2.8 female samples were presented. For the analyses of subsets of the experiments, the values deviated slightly (by <5%) from the above-mentioned values. Chi-square tests were used because they allow comparison with expected values that vary from case to case. This is a rather crude analysis, however, which shows only an overall pattern and does not account for repeated measures. To support the central finding of stronger responses to same-sexed scent marks, we also calculated generalized linear mixed models (GLMMs) with the penalized quasi-likelihood method and a binary error structure (Venables & Ripley 2002). We analysed which samples were more likely to elicit counter-marks and worry calls by males and females respectively. For these analyses, we only used experiments during which counter-marks (or worry calls respectively) had occurred. The models included donor category, sample type and donor sex as fixed factors and group identity as a random factor.

The effect of dominance on the likelihood of scent-marking and worry calling was also analysed in GLMMs with donor category, sex and location of the experiment as fixed factors and group and individual identity (nested within group) as random factors. For these analyses we only used experiments during which both dominants and subordinates had inspected the presented samples.

Data analysis was carried out in R 2.2.1 (R Development Core Team 2005) using the packages NLME (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002). Values are presented as $\bar{x} \pm 1$ SE.

Results

Inspection

The duration of inspection bouts was influenced by inspection order, donor category, sample type, donor sex, donor age category as well as sex and age category of the inspecting individual (for summary see Appendix, Table B). Samples of females were inspected longer than samples of males, in particular by males (Fig. 1a). Samples of older individuals were inspected longer than samples of younger individuals. This effect was restricted to adults and subadults and reversed for infants (Fig. 1b). Within adult donors, samples of dominant individuals were inspected longer than samples of subordinate individuals (LMM, $F_{1,2909} = 11.6$, $p = 0.0007$).

Males inspected the presented samples longer than females and were particularly interested in samples of females (Fig. 1a). Inspection effort varied among age categories with subadults inspecting samples longer than adults or infants (Fig. 1b). The increased inspection effort of subadults was directed equally to samples of the own and alien groups and to samples of same-sexed and opposite-sexed individuals (age × donor category × sex × donor sex interaction: $F_{1,4196} = 1.31$, $p = 0.26$; all lower interactions also not significant). Dominant and subordinate individuals spent equal time inspecting samples (LMM, $F_{1,2510} = 0.27$, $p = 0.60$).

Worry Calls

Worry calls were given almost exclusively by adults (adults: observed 268, expected 237.4 calls; subadults:

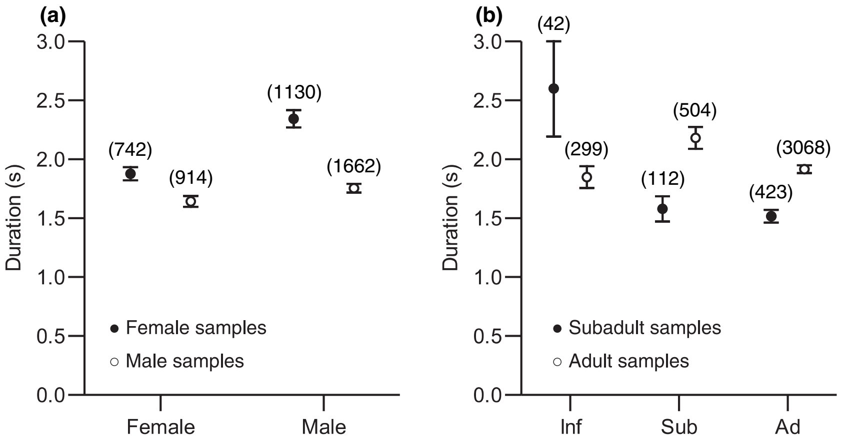

Fig. 1: Duration of single inspection bouts. (a) Inspection of female and male samples by females and males. (b) Inspection of subadult and adult samples by infants (Inf), subadults (Sub) and adults (Ad). $\bar{x} \pm$ SE are shown. Number of inspection bouts is given in brackets.

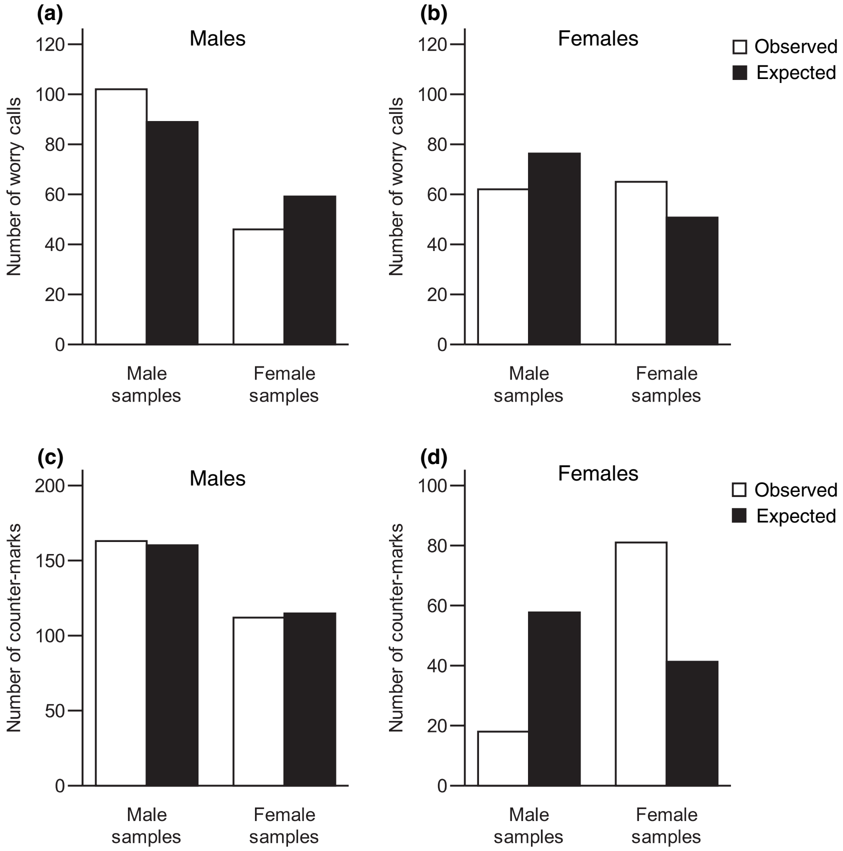

Fig. 2: Observed and expected frequencies of worry calls (a, b) and counter-marks (c, d) of males and females given in response to samples of males and females. Expected frequencies are based on the number of samples of each sex presented in the experiments.

observed 7, expected 37.6 calls; $\chi^2_{(1)} = 28.8$, $p < 0.001$). Within adults, dominant individuals were more likely to give worry calls than subordinate ones (GLMM, $F_{1,318} = 8.29$, $p = 0.0043$), but there was no sex difference ($F_{1,108} = 1.53$, $p = 0.22$). Males and females were more likely to give worry calls in response to samples of same-sexed individuals than to samples of opposite-sexed individuals (males: $\chi^2_{(1)} = 4.83$, $p = 0.028$, $n = 148$; females: $\chi^2_{(1)} = 6.71$, $p = 0.010$, $n = 127$; Fig. 2a, b). This was further corroborated by the finding that same-sexed samples were more likely to elicit worry calls than opposite-sexed samples from both males and females (Table 1).

Counter Marks

Of all counter-marks, 69% were placed on top of the original mark, 16% were placed clearly apart from the original mark and 15% were placed very close to the original mark but it could not be judged from the videotapes if the counter-mark covered the original mark or not. Counter-marks were mostly deposited by adults and rarely by subadults (adults:

Table 1: Factors affecting the probability that a sample elicited worry calls

Explanatory term	F statistic	df	p
Donor category (neighbour and stranger)	15.2 *2.90*	1, 303 *1, 295*	0.0001 *0.09*
Sample type (faeces and urine)	0.76 *6.95*	1, 303 *1, 295*	0.38 *0.009*
Donor sex (male and female)	4.92 *5.21*	1, 303 *1, 295*	0.03 *0.02*
Minimal model:			
	Effect size	SE	
Constant	−0.80 *−1.12*	0.40 *0.46*	
Donor category (stranger)	−1.10 *−0.47*	0.28 *0.28*	
Sample type (urine)	– *0.72*	– *0.27*	
Donor sex (male)	0.64 *−0.62*	0.28 *0.27*	

Only experiments during which worry calls occurred were included in this analysis. We separately analysed the probability that a sample elicited worry calls from males (upper row) and from females (lower row, italic).

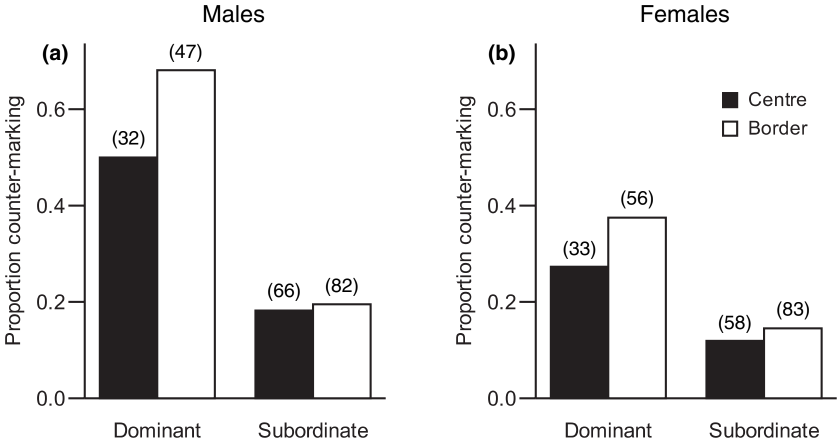

Fig. 3: Proportion of dominant and subordinate individuals counter-marking during experiments in the centre and at the border of the home range. (a) Males. (b) Females. Numbers in brackets give sample sizes.

observed 463, expected 404.6 counter-marks; subadults: observed 16, expected 74.4 counter-marks; $\chi^2_{(1)} = 54.3$, $p < 0.001$). Within adults, males were more likely to counter-mark than females (GLMM, $F_{1,106} = 6.1$, $p = 0.015$) and dominant individuals were more likely to counter-mark than subordinate ones ($F_{1,336} = 31.8$, $p < 0.001$). However, subordinates were still responsible for 27% of all counter-marks by adults to which a dominance status could be assigned. Subordinate and dominant individuals of both sexes were more likely to counter-mark during experiments at the border of the home range than in the centre ($F_{1,336} = 5.22$, $p = 0.023$; Fig. 3).

Males counter-marked more than females ($\chi^2_{(1)}=20.9$, $p < 0.001$) and targeted samples of both sexes equally ($\chi^2_{(1)} = 0.12$, $p = 0.73$, $n = 275$; Fig. 2c). Females, in contrast, counter-marked almost exclusively same-sexed samples ($\chi^2_{(1)} = 65.5$, $p < 0.001$, $n = 99$; Fig. 2d). When analysing the response to scent marks of the own group separately, we found that both males (27 of 30 marks; $\chi^2_{(1)} = 8.4$, $p = 0.004$) and females (9 of 14 marks; $\chi^2_{(1)} = 5.0$, $p = 0.026$) preferentially counter-marked same-sexed samples. This was further corroborated by the finding that female samples were more likely to get counter-marked by females than male samples, whereas male and female samples were equally likely to get counter-marked by males (Table 2).

Table 2: Factors affecting the probability that a sample was counter-marked

Explanatory term	F statistic	df	p
Donor category (neighbour, own and stranger)	0.54	2, 359	0.58
	3.29	*2, 361*	*0.04*
Sample type (faeces and urine)[a]	0.96	1, 359	0.33
	0.13	*1, 361*	*0.72*
Donor sex (male and female)	2.18	1, 359	0.14
	10.9	*1, 361*	*0.001*
Minimal model:			
	Effect size	SE	
Constant	−0.91	0.28	
	−1.60	*0.35*	
Donor category (own)	–	–	
	0.49	*0.38^{ns}*	
Donor category (stranger)	–	–	
	−0.83	*0.45*	
Donor sex (male)	–	–	
	−1.06	*0.35*	

Only experiments during which counter-marks occurred were included in this analysis. We separately analysed the probability that a sample was counter-marked by males (upper row) and by females (lower row, italic).

ns, not significant.

[a] When looking at only anal marks, urine samples were more likely to get counter-marked than faecal samples (GLMM, $F_{1,363} = 6.10$, $p = 0.014$). All other results remained qualitatively the same.

Influence of Oestrus on the Response

Donor group in oestrus

Compared with samples of non-oestrus females, samples of females in oestrus were inspected longer (oestrus samples: 4.31 ± 0.53 s, n = 52 inspection bouts; non-oestrus samples: 2.10 ± 0.05 s, n = 1820 inspection bouts; LMM, $F_{1,1663} = 22.5$, $p < 0.001$), particularly by males (sex × donor oestrus interaction: $F_{1,1663} = 8.8$, $p = 0.003$). Compared with non-oestrus samples, oestrus samples were also more likely to get counter-marked by females (Fisher's exact test: $p = 0.022$) but not by males ($p = 0.21$).

Acceptor group in oestrus

Females in oestrus spent more time inspecting the presented samples than non-oestrus females (oestrus females: 2.78 ± 0.30 s, n = 89 inspection bouts; non-oestrus females: 1.69 ± 0.03 s, n = 1457 inspection bouts; LMM, $F_{1,1470} = 26.7$, $p < 0.001$). This increased effort was directed equally to samples of males and females (oestrus × donor sex interaction $F_{1,1470} = 0.001$, $p = 0.99$). Females in oestrus showed a massive increase in their counter-marking rate compared with non-oestrus females, from 0.3 to 2.9 marks per individual and experiment (oestrus: observed 37, expected 5.1 counter-marks; non-oestrus: observed 94, expected 125.9 counter-marks; $\chi^2_{(1)} = 194.8$, $p < 0.001$), and they still targeted almost exclusively female samples (33 out of 35 counter-marks). However, this result largely depends on three females of a single group, which were responsible for 77% of the counter-marks observed during oestrus-experiments.

Males also increased their inspection effort, when the females of their own group were in oestrus (oestrus: 2.91 ± 0.20 s, $n = 226$ inspection bouts; no oestrus: 1.90 ± 0.04 s, $n = 2335$ inspection bouts; LMM, $F_{1,2441} = 20.0$, $p < 0.001$) and their increased effort was also directed equally to samples of males and females (oestrus × donor sex interaction $F_{1,2441} = 0.59$, $p = 0.44$). Males increased their counter-marking rate when the females of their own group were in oestrus, from 0.6 to 1.0 marks per individual and experiment (oestrus: observed 29 expected 18.9 counter-marks, no oestrus: observed 326, expected 336.1 counter-marks; $\chi^2_{(1)} = 5.70$, $p = 0.017$), but much less so than the females themselves did.

Discussion

We found good evidence that the main function of scent-marking in banded mongooses lies in intrasexual competition between and within groups. Both males and females counter-marked the presented samples and placed counter-marks mostly on top of the original marks (over-marks). Males counter-marked at higher rates, though the observed sex bias in counter-marking rates of 1.6 was small. Comparative data on sex-specific counter-marking rates are rare. Studies on scent-marking rates in other mammals are much more abundant and males commonly show 2–10 times higher rates than females (Johnson 1973; Begg et al. 2003; Lewis 2005; Jordan 2007). In an exceptionally extensive study, Hurst (1990) found that in mice also counter-marking rates are heavily male biased. The small sex bias in the banded mongoose may be related to considerable competition among females for breeding opportunities despite comparably low levels of reproductive skew. Furthermore, adults of both sexes responded more intensely to scent marks of same-sexed than to marks of opposite-sexed individuals. In particular, both males and females were more likely to give worry calls in response to scent marks of same-sexed individuals than to marks of opposite-sexed individuals. As worry calls were only given to samples of neighbouring groups and strangers, this reflects intrasexual competition between groups. Also, females counter-marked almost exclusively female scent marks and most counter-marks were placed on top rather than next to the original mark. Males preferentially counter-marked same-sexed scent marks when presented with samples of the own group, but counter-marked scent marks of both sexes equally when presented with samples of other groups. This indicates that, like in meadow voles (*Microtus pennsylvanicus*) (Ferkin 1999), the two sexes may use different counter-marking strategies. As the top scent mark may be preferred by potential mates, as demonstrated in hamsters and voles (Johnston et al. 1994, 1997), over-marking scent marks of same-sexed competitors likely improves access to mates.

Further support for the intrasexual competition hypothesis comes from the influence of oestrus on the responses to scent marks. Samples of females in oestrus were inspected longer by males and counter-marked more by females. Females in oestrus increased their inspection effort as well as their counter-marking rate. Also males increased their inspection effort and their counter-marking rate (though less markedly), when the resident females were in oestrus.

We found little evidence that scent-marking is a form of self-advertisement to potential mates in banded mongooses. First, contrary to the prediction of the self-advertisement hypothesis, most counter-marks were placed on top of the original marks rather than next to it. Second, females showed an increase in marking behaviour during oestrus and males also increased their scent-marking rate when the resident females were in oestrus. These patterns have been found in a variety of mammals and it is commonly assumed that they are a sign of females advertising their receptivity (Ferkin et al. 2004). However, it might also reflect intrasexual competition, which is particularly intense during oestrus. Third, subadult individuals spent more time investigating the presented excreta than adults did. However, the increased inspection effort of subadults was found equally in response to samples of neighbours, strangers and the own group and equally to same-sexed and opposite-sexed individuals. Thus, it might reflect lack of experience rather than the checking of mating or dispersal opportunities. Finally, subordinate individuals showed slightly higher marking rates in experiments at the border of the home ranges compared with the centre. However, this increase was even more pronounced for dominant individuals. We cannot exclude that both subordinates and dominants advertise themselves to opposite-sexed individuals in neighbouring groups. Alternatively, the observed pattern might reflect that scent-marking in banded mongooses still plays a role in territory demarcation. The self-advertisement hypothesis also predicts that subordinate individuals should increase scent-marking rates during interactions with neighbouring groups. This could not be tested in the present study.

In an other herpestid, the yellow mongoose (*Cynictis penicillata*), self-advertisement was found to be a central function of scent-marking (Wenhold & Rasa 1994) and also in meerkats there is some evidence that scent-marking plays a role in self-advertisement (Jordan 2007). Rasa's (1973) extensive study on scent-marking in a captive family of dwarf mongooses (*Helogale parvula*) does not allow conclusions regarding intrasexual competition and self-advertisement. The contrast between banded mongooses, meerkats and yellow mongooses is likely explained by differences in the social systems of these species: First, yellow mongooses of both sexes disperse from their natal group (Wenhold 1990) and also male meerkats commonly do not breed in their natal group, in which only related partners are available, but have to disperse to gain breeding opportunities (O'Riain et al. 2000). In banded mongooses, in contrast, both sexes regularly breed in their natal group and matings between close relatives are common (Cant 1998; Gilchrist 2001). Whether banded mongooses use scent-marking to advertise themselves when they have been evicted from their natal group remains to be investigated. Second, subordinate male meerkats frequently leave their group temporarily to seek matings with females of other groups (Young et al. 2005). In banded mongooses, such 'roving' behaviour is not observed and matings between members of different groups only occur when two groups meet and fight (Cant et al. 2002). Both factors probably contribute to subordinate yellow mongooses and meerkats having more motivation to advertise themselves to members of neighbouring groups than subordinate banded mongooses. Support for the self-advertisement hypothesis has also been found in other species in which the mating system likely makes mate attraction crucial for reproductive success, for example in promiscuous male meadow voles and in unpaired monogamous male prairie voles (*Microtus ochrogaster*) (Thomas & Wolff 2002; Wolff et al. 2002). Also subordinate female marmosets (*Callithrix jacchus*) show evidence for self-advertisement and their potential mates are most likely encountered in neighbouring groups (Heymann 2006).

Finally, dominant banded mongooses of both sexes counter-marked more than subordinate individuals. This was predicted by the dominance assertion hypothesis but it can also be explained by intrasexual competition as our definition of dominance is tightly linked to behaviour of intrasexual competition. Moreover, a considerable proportion of subordinates (on average 16% compared with 46% of dominants, see Fig. 3) showed counter-marking during the experiments, which cannot be explained as dominance behaviour.

In conclusion, we found strong support for the hypothesis that the main function of scent-marking in banded mongooses lies in intrasexual competition both between and within groups, whereas we found little evidence for self-advertisement. Additionally, scent-marking possibly plays a role in territory defence and may be involved in dominance behaviour. However, dominance assertion is unlikely to be the main motivation for marking, as reproduction is not monopolized by a dominant pair in this species. Our findings are in agreement with a number of studies on the functions of scent-marking in social mammals (Ralls 1971; Wenhold & Rasa 1994; Heymann 2006) which found that scent-marking serves multiple purposes and that probably mate attraction and intrasexual competition rather than territory defence are the main motivation of scent-marking in these species. Our results indicate that differences in the social system, particularly in regard to natal dispersal, may shift the main function of scent-marking from self-advertisement and mate attraction to intrasexual competition.

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Appendix

Table A: Sample sizes of the analyses of inspection, worry calls and counter-marks in the order they appear in the Results section

Analysis	Observations[a]	Experiments	Groups	Individuals[b]
Inspection				
Inspection (LMM)	4448	74	7	208
Inspection – donor status (LMM)	3128	72	7	204
Inspection – dominance (LMM)	2641	74	7	122
Worry calls				
Worry calls (age, χ^2-test)	275	65	7	70
Worry calls – dominance (GLMM)	435	56	7	116
Worry calls by males (χ^2-test)	148	43	7	43
Worry calls by females (χ^2-test)	127	42	7	27
Worry calls by males (GLMM)	313	51	7	NA
Worry calls by females (GLMM)	304	48	7	NA
Counter-marks				
Counter-marks (age, χ^2-test)	479	62	7	103

Table A: (continued)

Analysis	Observations[a]	Experiments	Groups	Individuals[b]
Counter-marks – dominance (GLMM)	457	56	7	114
Counter-marks by males (χ^2-test)	275	50	7	59
Counter-marks by females (χ^2-test)	99	25	6	27
Counter-marks by males (GLMM)	371	56	7	NA
Counter-marks by females (GLMM)	373	56	7	NA
Donor group in oestrus[c]				
Inspection of female samples (LMM)	52/1820	5/70	4/7	30/197
Counter-marks (Fisher's exact test)	9/184	5/62	4/7	NA
Acceptor group in oestrus[c]				
Inspection by females (LMM)	89/1457	4/74	3/7	9/64
Counter-marks by females (χ^2-test)	37/94	4/30	3/6	7/27
Inspection by males (LMM)	226/2335	5/66	3/7	32/108
Counter-marks by males (χ^2-test)	29/326	4/52	3/7	10/72

[a] For linear mixed models (LMMs), number of observations is the number of inspection bouts. For generalized linear mixed models (GLMMs), it is either the number of samples presented or the number of individuals present. For χ^2-tests, it is the number of worry calls or counter-marks observed.

[b] NA, not applicable, analysis on group level. For χ^2-tests, number of individuals showing the response (rather than number of individuals present) is given.

[c] Numbers are given as oestrus/non-oestrus.

Table B: Factors affecting the duration of single inspection bouts. Interaction terms are given only if significant. The analysis was conducted on 4448 inspection bouts of 208 individuals in seven groups

Explanatory term	F statistic	df	p
Inspection order	69.7	1, 4222	<0.0001
Donor category (neighbour, own and stranger)	21.5	2, 4222	<0.0001
Sample type (faeces and urine)	205.2	1, 4222	<0.0001
Donor sex (male and female)	77.1	1, 4222	<0.0001
Donor age category (adult and subadult)	7.01	1, 4222	0.008
Sex (male, female)	4.50	1, 200	0.035
Age category (adult, subadult and infant)	4.16	2, 4222	0.016
Donor sex × sample type	47.5	1, 4222	<0.0001
Age category × sample type	7.18	2, 4222	0.0008
Age category × donor age	5.37	2, 4222	0.005
Age category × inspection order	5.06	2, 4222	0.006

Minimal model	Effect size	SE
Constant	1.235	0.029
Inspection order	−0.013	0.0016
Donor category (own)	−0.110	0.017
Donor category (stranger)	−0.039	0.014
Sample type (urine)	0.210	0.016
Donor sex (male)	−0.029	0.013
Donor age (subadult)	−0.038	0.017
Sex (male)	0.037	0.017
Age category (infant)	−0.173	0.037
Age category (subadult)	0.069	0.030
Donor sex (male) × sample type (urine)	−0.139	0.020
Age category (infant) × sample type (urine)	0.141	0.037
Age category (subadult) × sample type (urine)	0.019	0.029^{ns}
Age category (infant) × donor age (subadult)	0.164	0.056
Age category (subadult) × donor age (subadult)	−0.041	0.038^{ns}
Age category (infant) × inspection order	0.030	0.012
Age category (subadult) × inspection order	−0.009	0.005^{ns}

ns, not significant.