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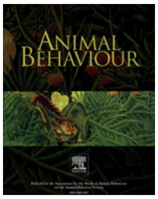

Scent marking in wild banded mongooses: 3. Intrasexual overmarking in females

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In contrast to numerous studies of scent marking in male mammals, studies of female scent marking are relatively rare. We have previously shown that communally breeding female banded mongooses, *Mungos mungo*, are more likely to overmark the scent of other females. Here we describe female overmarking patterns in more detail, and discuss these results in relation to hypotheses potentially explaining such 'female intrasexual overmarking'. To our knowledge, this is the first study to investigate female overmarking in any wild mammal. First, although we found some evidence of individually distinctive scent marks in females, we found no evidence to suggest that female intrasexual overmarking was related to competition for food, as feeding competition was infrequent, and unrelated to overmarking scores. We also found no evidence to suggest that intrasexual overmarking in females was involved in reproductive suppression. Females with the highest and lowest overmarking scores in each group were mate-guarded by males for similar durations. Finally, we found little evidence to suggest that female intrasexual overmarking was involved in competition for males. Although the female with the highest overmarking score in each group tended to be mate-guarded by males in better condition than the female with the lowest overmarking score, a female's overmarking score affected neither the amount of harassment she received from males nor the frequency of mating attempts received. These results are discussed in light of these and other untested hypotheses for female overmarking.

Overmarking is the placement of a scent mark directly on top of the scent mark of another individual (Johnston et al. 1994), and individuals of some species seem to have developed specialist mechanisms to determine which individual's mark is on top (reviewed in Johnston 2005). In laboratory studies where this has been investigated, individuals showed a preferential memory for individuals whose mark was on top, regardless of the degree of scent overlap (e.g. golden hamsters, *Mesocricetus auratus*: Johnston & Bhorade 1998). This suggests a selective preference for top-scent donors rather than a masking effect (see Johnston et al. 1995; Johnston 2005). Female meadow voles, *Microtus pennsylvanicus*, seem to prefer to associate with males whose mark is on top (Johnston et al. 1997), and in some other species females even seem to mate preferentially with such top-scent males (pygmy loris, *Nycticebus pygmaeus*: Fisher et al. 2003). Like patterns of scent marking in general (reviewed in Ralls 1971; Gosling & Roberts 2001), males seem to overmark more than females in some species (e.g. meerkats, *Suricata suricatta*: Jordan 2007), and overmarking appears to be associated with the acquisition and defence of mates and mating opportunities (e.g. meadow voles: Johnston et al. 1997), although a number of other potential hypotheses have been suggested (reviewed in Ferkin & Pierce 2007). In contrast to male scent marking, studies of overmarking by females are relatively rare (but for exceptions see Johnston 1977; Hurst 1990; Wolff et al. 2002), and therefore this represents an overlooked and potentially important area of scent-marking research, particularly in the natural environment.

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Banded mongooses, *Mungos mungo*, present an opportunity to investigate the function of female overmarking. They live in large, stable, territorial groups, within which scent marking is common (Jordan et al. 2010). Both sexes overmark frequently, preferentially overmarking the scents of same-sex individuals (Müller & Manser 2008a; Jordan et al. 2011a). Within groups, multiple males and females reproduce synchronously in each breeding attempt during oestrous periods lasting an average of 6 days (Rood 1975; Cant 2000). Males compete for access to receptive females (Cant 2000), and 83% of adult females become pregnant in each breeding attempt (Cant 2000; Gilchrist et al. 2004), giving birth to communal litters (Cant 2000). Although other functional hypotheses have been suggested for overmarking (reviewed in Ferkin & Pierce 2007), we have identified and developed three hypotheses that may be most relevant in this particular social system: (1) food competition, (2) mate competition and (3) reproductive suppression.

As maternal condition is likely to be an important determinant of female reproductive success (see Mousseau & Fox 1998), competition for food may drive patterns of female scent-marking behaviour, and such competition might be expected to be more frequent in the breeding season when nutritional demands are higher, or in periods of food scarcity. In many species, scent-marking sites are frequently associated with feeding sites (e.g. striped hyaena, *Hyaena hyaena*: Macdonald 1978; callitrichid primates: Lacher et al. 1981; Rylands 1985; African palm civet, *Nandinia binotata*: Charles-Dominique 1978). However, it is not yet known whether females invest disproportionately to males in scent marking food sources, nor whether defence of food sources can explain patterns of overmarking in females. Banded mongooses forage together as a group, fanning out and searching through leaf litter for small invertebrate prey (Rood 1975), but except when dependent young are fed, food items are never shared. If intrasexual overmarking in females is related to the acquisition of resources necessary to breed and rear offspring (see Clutton-Brock 2009), we might expect females that overmark more to be challenged less frequently for food items than females that overmark less.

Alternatively, in the mate competition (or mate attraction) hypothesis, females might preferentially overmark the scents of other females if this functions to signal their quality to males and allow them access to higher-quality mates. Although some authors have suggested that such a function would result in individuals overmarking the scents of opposite-sex individuals (Ferkin & Pierce 2007), in social species such as banded mongooses, placing your scent on top of that of same-sex rivals might be a form of advertising your own condition (Rich & Hurst 1998, 1999; Gosling & Roberts 2001; Jordan et al. 2011b), particularly if high-quality individuals are better able to afford the costs of continually overmarking their rivals (see Rich & Hurst 1998, 1999; Gosling & Roberts 2001). Although male mammals are generally more likely to compete for females (see Trivers 1972), in certain circumstances females may compete for mating opportunities with males (see Clutton-Brock 2009). For example, intrasexual competition between females for mates may be expected where males provide extensive parental care (e.g. Western Australian sea horse, *Hippocampus subelongatus*: Kvarnemo et al. 2007) or where the most preferred male is unable to service all females (e.g. topi, *Damaliscus korrigum*: Bro-Jørgensen 2007). In banded mongooses, both of these conditions are fulfilled, and so a degree of male mate choice and female competition for males may be expected. As oestrus is highly synchronous within groups (Cant 2000), a single male may be unable to monopolize access to all females. Additionally, males provide a high degree of paternal care by 'babysitting', 'escorting' and feeding dependent pups (Rood 1974, 1975; Cant 2003; Gilchrist 2004; Hodge 2005). In species of callitrichid primates where male care exceeds female care, rates of scent marking are strongly female biased (Heymann 2003), and intrasexual overmarking also occurs in females of these species (see Heymann 2003). Although this is unlikely to be true in all species, attracting a high-quality male may therefore be of prime importance in banded mongooses, and males might also benefit by competing for those particular females with high overmarking scores, as higher-quality females may produce more (see Gilchrist et al. 2004) or higher-quality offspring. If competition for males explains intrasexual overmarking by females, we would expect males to compete more intensively for females with higher overmarking scores, perhaps harassing them more during oestrus and attempting to mate with them more frequently. We might also expect to see females scent marking more frequently during breeding periods, as is the case for vaginal marking in golden hamsters (Johnston 1977).

A third hypothesis is that female overmarking is involved in reproductive suppression, and this may be most likely in a social species with competition over breeding. As the 'priming' effects of scents on other individuals are well known (reviewed in Brown 1985), it is possible that female overmarking might be employed as a tactic in reproductive suppression. Scents may have promotional (e.g. puberty acceleration, house mouse, *Mus musculus*: Massey & Vandenbergh 1981) or suppressive effects on recipients (e.g. puberty delay, house mouse: Massey & Vandenbergh 1980). As female scent marks placed on or in the vicinity of the scents of other females are likely to ensure that their own scent marks predominate in the environment, overmarking female scents may protect females from the primer cues produced by other females (Hurst 1990), although it is perhaps more likely to increase the efficacy of their own primer cues. If female intrasexual overmarking is a tactic employed to suppress other females, we would predict that females with higher overmarking scores might: (1) first breed at a younger age, and (2) delay their oestrus less, as there are potential fitness costs to delaying oestrus in banded mongooses. Most females give birth on the same day as each other regardless of their conception date (Cant 2000), which means that females that breed later have significantly shorter gestation periods (Cant 2000), potentially affecting pup size at emergence, which is known to have downstream fitness consequences (Hodge 2005).

We attempted to evaluate the function of scent marking in female banded mongooses, primarily by investigating the above three hypotheses. We did this by using behavioural observations of female overmarking behaviour in the field, and determining the chemical composition of multiple scent marks collected from individual females to assess whether each female has an individually recognizable scent profile. As overmarking score is likely to be correlated with other aspects of female quality likely to affect foraging challenges or breeding success, such as age and weight, we simultaneously controlled for these in our analyses. To the best of our knowledge, this study is the only evaluation of female–female overmarking in wild mammals to date, and as such it should provide a useful foundation on which future studies of female overmarking can be conducted in the natural environment.

METHODS

The general methods were identical to those described in the first paper in this series (Jordan et al. 2011a) except for the following differences and additions.

Scent Collection and Composition Analysis

To determine whether females had individually specific scents, we live-trapped 33 females from eight groups between December 2005 and October 2007, following the standard procedure (see

Jordan et al. 2011a). Four anal gland secretion (AGS) samples were collected from each female during different trapping events, with the first and last scents from the same female collected a mean ± SD 311.4 ± 154.6 days apart (range 92–593). Scent storage and analysis details are given in Jordan et al. (2011a). We weighed trapped females prior to recovery from anaesthesia, and additional weights were collected for the more habituated individuals in six social groups in the morning soon after emergence from the den. Individuals were tempted over to an electronic balance (models: Ohaus CT6000 and Sartorius TE4101) in the field with scraps of blended solid food waste, and were picked up by the scruff of the neck and placed on to the balance, where they were given a drop of powdered milk dispensed from a hamster bottle to persuade them to remain there while their weight was taken.

Behavioural Observations

Scent-marking and overmarking events were recorded by critical incident sampling (Altmann 1974), with overmarking defined as the placement of a scent mark on an existing scent mark produced by another individual within the same observation period, so that the two scents are at least partially overlapping (sensu Johnston et al. 1994). Each scent location was given a unique identifying number (the 'scent station'), and all investigation (sniffing or licking) and overmarking by subsequent visitors to each scent station were recorded, in order, until the group moved away from the site. It was often possible to observe all individuals at a scent-marking site, but on occasions when this was not possible, we focused on a smaller number of scent stations during the marking bout to ensure that no marks placed there were missed. We estimated each individual female's 'intrasexual overmarking score' as the proportion of encountered adult female scent marks that each female overmarked. Analyses only included females that were observed to encounter 10 or more scents deposited by other adult females throughout the study period. Encounters with a female scent included all instances of sniffing or licking individual scents and overmarks where the top or most recent marker was another adult female, as previous results suggested that the top scent seems most important in determining overmarking response (Jordan et al. 2011a).

Competition for food

To investigate whether individuals were more or less likely to enter into foraging competition with females according to their intrasexual overmarking score, we calculated the relative number of foraging challenges directed towards females by other individuals. This was calculated for each female by subtracting the proportion of the group's total foraging challenges that each adult female would be expected to receive by chance from the proportion of foraging challenges that were observed to be directed towards that female (see Appendix Table A1). Expected values were calculated by dividing the frequency of foraging challenges directed towards all females by the number of females in the group. Only females that were adult at the start of the study and survived until the end of the study were included, to ensure they had equal opportunity to be challenged. We conducted three separate analyses involving approaches by (1) adult females, (2) adult males and (3) all adults. Foraging challenges included all observed instances where an individual was approached while in possession of a food item or foraging hole and responded by either blocking the approach of the other animal, snapping at the challenger, chasing off the challenger, pushing (or pulling) over the food item or foraging position, to actual physical fighting involving biting. In addition, we would have liked to test whether females overmark most often during times of food scarcity; however, these data were not available.

Competition for mates

Within groups, multiple females come into oestrus over a period of a few days, and males compete for access to them (Cant 2000). Some males act as 'mate-guards' by consistently following receptive females, staying within 2 m and aggressively attacking all other males that come within range (Cant 2000). Adult males that are unable to monopolize females in this way are 'nonguards', following females and their guards and attempting to sneak copulate (Cant 2000). The period from the first to the last observed instance of mate guarding in a group was termed 'group oestrus' (Cant 2000), and data were collected during 73 group oestrous periods in nine groups (mean ± SD = 8.11 ± 5.37 per group, range 2–16). An 'oestrous session' was any morning or afternoon observation session within a group oestrous period where at least one female was mate-guarded by a male.

To determine whether females overmarked each other to signal their quality to potential mates, behavioural estimates of male–male competition over each female were recorded using a combination of critical incident sampling and 20 min focal watches. During group oestrus, all mating attempts were recorded on occurrence using a hand-held Psion II data logger (model LZ-64). A 'mating attempt' involved the male grabbing the female around the waist and attempting to climb onto her from the rear. A mating attempt that was uninterrupted for 30 s or more was scored as a 'mating' (Cant 2000). Analyses of mating attempts included 26 adult females receiving five or more. During focal watches of oestrous females, the identity of all males within 2 m of the focal female was recorded each minute, allowing the mean number of males within 2 m of each female to be calculated for each oestrous session as an estimate of 'harassment' by males. To account for variation in the number of oestrous females in each group and in each group oestrous session within groups, harassment was calculated as the number of adult males per oestrous female subtracted from the mean number of males <2 m from females in that session. Harassment values were only included in analyses if they were based on 10 or more scans in each oestrous session.

In addition, 426 instances of direct male–male competition for 29 females were recorded in six groups. Direct male–male competition varied from blocking, which involved one male turning to shield the female from an approaching male, through chasing another male away from a female, to physical fighting, which included biting. Using all male–male competition involving adults, we extracted frequencies for each adult female that survived to the end of the study period, to ensure that they presented an equal opportunity to be competed over. To control for differences in the number of females and the number of instances of competition across groups, each female's male–male competition score was calculated as the proportion of the group's competition that each female received minus the proportion of competition expected by chance (1/number of adult females in the group present throughout the study; Appendix Table A1).

Finally, to determine whether females with higher intrasexual overmarking scores were mate-guarded by males with different characteristics to those males mate guarding females with lower overmarking scores (e.g. weight, age), we extracted data for the females with the highest and lowest overmarking scores in each of six groups (where focal watches could be conducted). In each oestrous session, all mate-guarded females and the identity of their mate-guard were recorded, and paired *t* tests were conducted on the female's mate-guard's (1) mean age, (2) mean weight and (3) mean condition. The mean condition of males that a female was mate-guarded by was estimated using the standardized residuals of a regression of male age on male weight for all males that were adult at the beginning of the study. To calculate each female's ‘mate-guard’s mean age’, the age (in days) of a female’s mate-guard was noted each session. The sum of these ages was divided by the number of sessions during which the female was mate-guarded. Similarly, a female’s ‘mate-guard’s mean weight’ was calculated by summing the weight of each of her mate-guards collected on or closest to the morning of the session that that particular male mate-guarded the female, and divided by the number of sessions that the female was guarded by a weighed male.

Reproductive suppression

To investigate whether female intrasexual overmarking might be a form of female–female suppression, we asked whether overmarking score was related to delay in oestrus. To assess this, we calculated the mean delay in oestrus for 30 females that were mate-guarded in two or more oestrous periods with at least one other female. ‘Mean delay in oestrus’ for each female was estimated as the mean number of days the female was first mate-guarded after the first female in the group (Table A1). As excluding females that were not mate-guarded at all during a group oestrous period would underestimate any suppression effect, females that were not mate-guarded in a given oestrous period were given a delay score equal the total length of the oestrous period. Similarly, we also compared the ‘mean duration of oestrus’ for each female, including zero values for oestrous periods in that group where the female was not mate-guarded (Table A1). Only oestrous periods where at least two females were mate-guarded were included in these analyses, and linear mixed models were conducted to control for repeated measures and the potentially confounding effects of female age and weight. Finally, paired *t* tests were conducted on the females with the highest and lowest overmarking scores, respectively, in each of the six groups.

Statistical Analyses

Scent mark composition

Chemical data were analysed following chemical and statistical methods described in detail in Jordan et al. (2011a). Log-transformed percentage abundances were derived from absolute abundances of 35 discrete compounds, which were reduced and made independent by entering them into a principal components analysis (PCA). For all 33 females, a discriminant function analysis (DFA) was conducted by simultaneously entering the principal components derived using the Kaiser method (Kaiser 1960). Post hoc ‘bootstrapping’ analyses were conducted in ‘R’ (R Development Core Team 2008) on the results of the DFA. This allowed us to determine the probability that a cross-validated correct assignment value was achieved by chance, and we followed the methods of Müller & Manser (2008b).

Behavioural observations

Linear mixed models (LMMs) were conducted in Genstat 8.1 (Rothamstead Experimental Station, Harpenden, U.K.). Mixed models are similar to general linear models (GLM), but allow both fixed and random effects to be fitted, with random terms controlling for repeated measures such as individual and group (Schall 1991). All potential explanatory terms, both factors and variates, were entered into the model and dropped sequentially until only those terms that explained significant variation in the data remained. This approach was particularly important here, as it allowed potentially confounding factors, such as a female’s age and weight to be accounted for when estimating the effect of intrasexual overmarking score. For main effects, all two-way interactions were tested, but were sequentially dropped and were only included in tables if found to explain significant variation ($P < 0.05$). The process was repeated by the additive method (sequential adding of terms with the retention of terms only if their addition significantly increased explained variance) to confirm the structure of the model (Russell et al. 2002). Wald statistics and probability values for significant terms were derived with all significant terms in the model, while values for nonsignificant terms were obtained by adding each term individually to the minimal model. The significance levels of all explanatory variables and significant two-way interactions are shown in model tables. For factorial terms, differences in average effects are shown relative to one level of the factor, which is set to zero.

RESULTS

Scent Mark Composition

To determine whether anal gland secretions were individually specific, we statistically compared the chemical profiles of 33 adult females, each sampled four times. Following a PCA, a DFA was conducted by simultaneously entering 11 principal components (which explained 70.8% of the variance). The corresponding DFA assigned 15.9% of the cross-validated samples to the correct individual, which is significantly greater than the 3.0% expected by chance (Table 1). As individual discrimination is likely to be most important within social groups, we conducted DFAs for females within groups. The corresponding DFAs assigned a significantly greater percentage of the cross-validated samples to the correct individual than would be expected by chance in one group (group D), but not another (group B; Table 1). Figure 1 shows chromatograms for two adult females, with each female sampled twice for comparison. Figure 2 shows DFA plots for repeated samples from all females in group D. Other groups did not produce a sufficient number of samples from a sufficient number of females to allow statistical comparison.

Behavioural Observations

Female banded mongooses preferentially overmark encountered scents of same-sex group mates (Jordan et al. 2011a), but the

Table 1
Summary of discriminant function analyses (DFA) for all females in the population and females from two social groups independently, showing the significance of post hoc bootstrapping analyses on the percentage correct assignment

Individuals included in analysis	No. of females	No. of samples/female	PCs/% variance explained	% Assignment expected by chance	% Correct assignment (cross-validated)	*P* (bootstrapping)
All females	33	4	11/70.8	3.0	15.9	<0.0001
Group B	6	4	9/85.9	16.7	25.0	0.188
Group D	7	4	11/87.9	14.3	50.0	<0.0001

Also shown are the number of principal components (PCs) entered into the DFA, and the percentage variance they encapsulate from 35 detected compounds in the raw secretions.

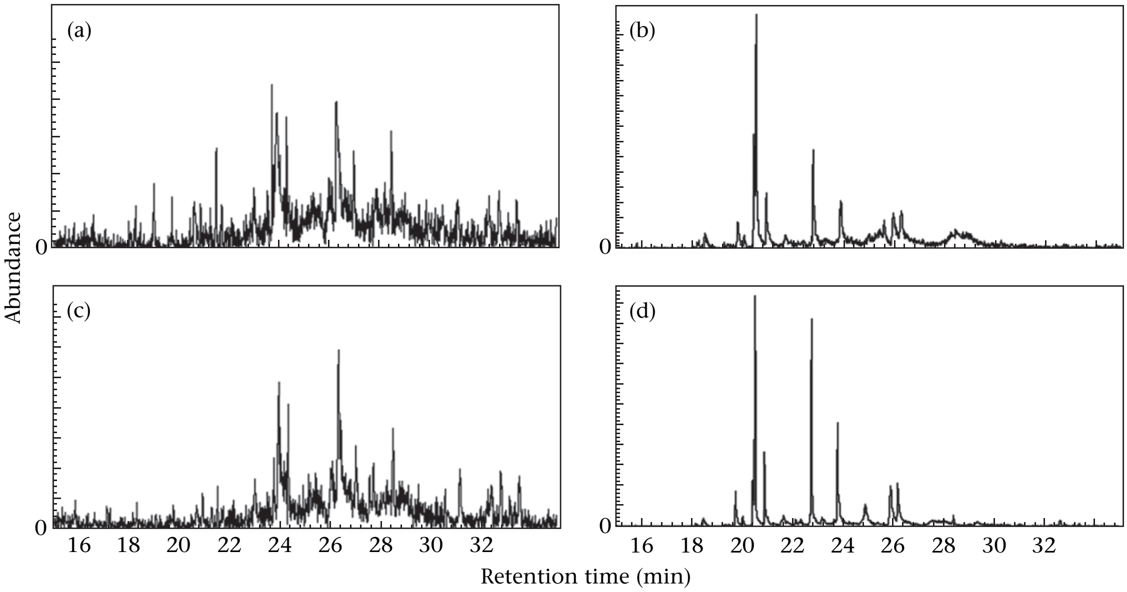

Figure 1. Gas chromatography–mass spectroscopy profiles for anal gland secretions from two adult females: (a, c) BF214 and (b, d) FF058. Samples were taken in (a, b) January 2006 and (c, d) April–May 2006. In each chromatogram, elution time from the column is plotted against abundance, with each spike representing a particular chemical compound.

degree to which individual females overmarked female scents (their intrasexual overmarking score) varied. Overall, of 1003 encounters of female scents by female mongooses, 857 (85.6%) resulted in overmarking, and the 38 females that encountered 10 or more female scent marks overmarked between 60 and 100% of these (85.2 ± 1.14%).

In the appropriate subset of data, females with the highest overmarking score in each group overmarked 88.3 ± 3.90% (range 70.0–97.0) of encountered female scents, whereas the female with the lowest overmarking score overmarked 73.8 ± 4.9% (range 60.0–91.0).

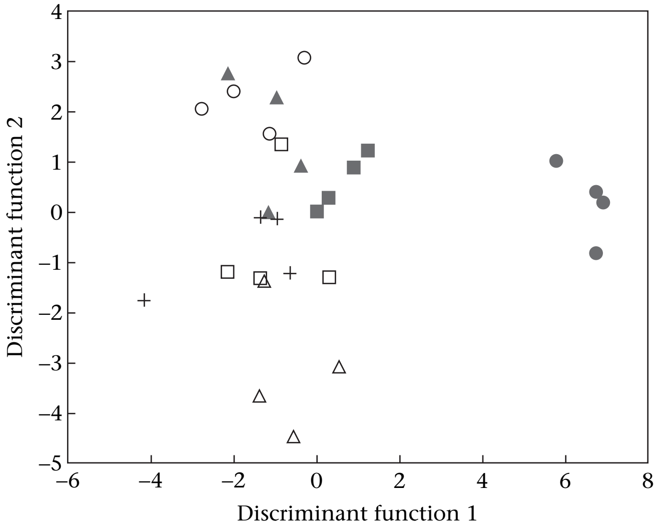

Figure 2. Plot of discriminant function scores for anal gland secretions collected from adult female banded mongooses from group D (DF022 [△], DF024 [○], DF026 [□], DF045 [▲], DF051 [●], DF055 [■], DF056 [+]). Each individual contributed four scent samples to the data set (December 2005–April 2006). DFA was performed on 11 principal components generated by PCA (correlation matrix) on log-transformed percentage abundances (percentage of total compounds eluted from 10 to 37 min) of 35 distinct compounds eluted during gas chromatography–mass spectroscopy analyses.

Competition for food

We recorded 63 foraging challenges involving 26 females, and a GLM showed that the number of foraging challenges a female received relative to other females in the group was not related to the female's overmarking score (Fig. 3), weight or age for foraging challenges with other adult females, adult males, or with adults of both sexes combined (Tables A2–A4). We therefore found no

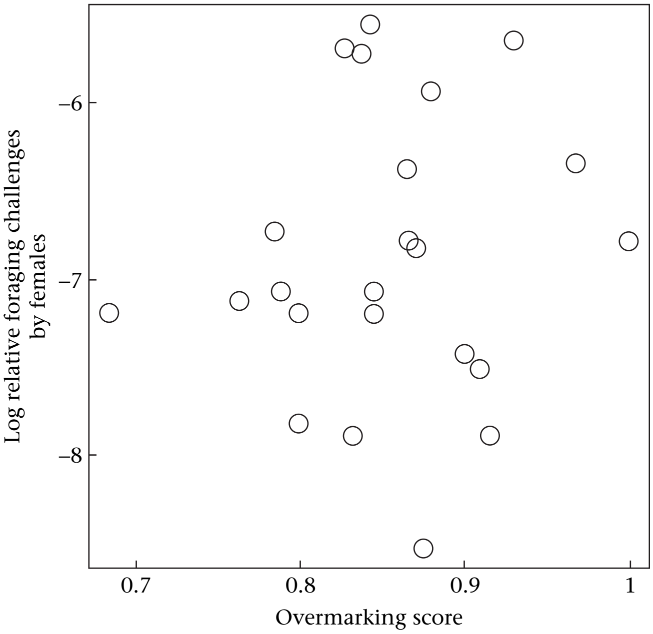

Figure 3. Data from a linear regression showing no relationship between a female's overmarking score and the relative number of foraging challenges by other females that female received. 'Relative foraging challenge' for each female was the proportion of the group's total foraging challenges that each adult female should receive by chance subtracted from the proportion of foraging challenges that were observed to be directed towards that female. These data are based on 63 foraging challenges involving 26 females from five groups.

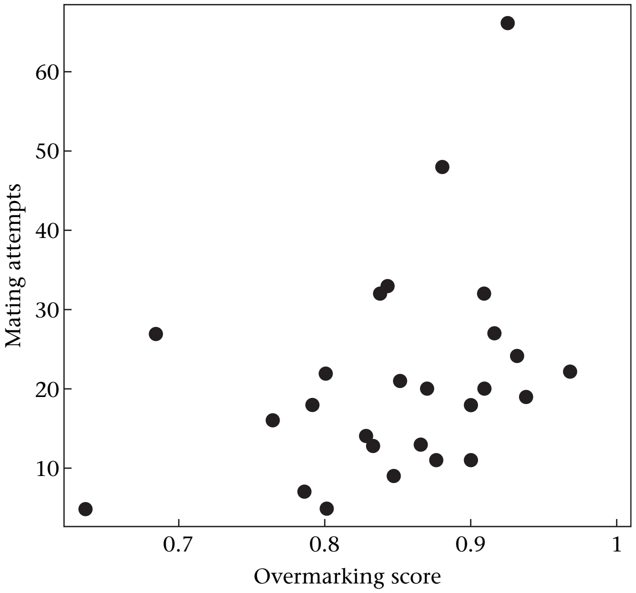

Figure 4. Data from a linear regression showing the relationship between female intrasexual overmarking score and the number of mating attempts by males.

evidence to suggest that females were approached over food according to their overmarking score or that females that were less harassed over food items overmarked a greater proportion of encountered scents.

Competition for mates

Although there was a nonsignificant positive tendency for females with a higher overmarking score to receive an increased number of mating attempts from males (linear regression: $r^2 = 0.126$, $N = 26$, $P = 0.075$; Fig. 4), the degree of 'harassment' of females by males during their oestrous period was not affected by the female's overmarking score. A linear mixed model controlling for repeated measures of 'group', 'female identity', 'male identity' and 'group oestrous period' showed that the 'harassment' received by a female was affected by the number of oestrous females in the group (Table 2). As the number of oestrous females decreased, their per capita harassment by males increased as expected, but by controlling for this we were able to show that a female's intrasexual overmarking score did not explain the degree of harassment it received from males (Table 2). As an effect of overmarking on harassment may arise because overmarking females are older and potentially of better quality, female age and weight were incorporated in the model as covariates but neither significantly explained the harassment received by males (Table 2).

Table 2
Linear mixed model showing the factors affecting harassment of females by males during oestrous periods

	Wald statistic (χ^2)	*df*	*P*
Full model			
Number of oestrous females	11.97	1	<0.001
Weight	0.24	1	0.626
Age	0.64	1	0.427
Intrasexual overmarking index	0.00	1	0.957
Minimal model	Coefficient estimate	SE	
Constant	1.034	0.060	
Number of oestrous females	−0.059	0.017	

Harassment was measured as the number of males within 2 m minus the number of adult males per oestrous female in that session ($N = 166$ sessions), and analyses were conducted during 29 group oestrous periods involving 28 females guarded by 40 males in five groups. To control for repeated measures, 'group' (estimated variance component = 0.011, SE = 0.012), 'female identity' (estimated variance component = 0.006, SE = 0.005), 'male identity' (estimated variance component = 0.005, SE = 0.006) and 'group oestrous period'. Coefficient estimates represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size.

The frequency of direct competition events between males for females was not affected by the overmarking score of females. There was no correlation between a female's intrasexual overmarking score and its 'relative male–male competition' score (linear regression: $r^2 = 0.023$, $N = 29$, $P = 0.445$), or the number of instances of male–male competition for that female per adult male per hour of focal observation ($r^2 = 0.015$, $N = 28$, $P = 0.534$). Although the females with the highest overmarking score in each group were mate-guarded by males of similar mean age (paired *t* test: $t_5 = -0.620$, $N = 6$, $P = 0.562$) and mean weight ($t_5 = 1.341$, $N = 6$, $P = 0.238$) to the females with the lowest overmarking score in the same group, they were mate-guarded by males in better mean 'condition' ($t_5 = 4.353$, $N = 6$, $P = 0.007$).

To assess the possibility that any effects might have been caused by differences in female quality aside from female overmarking score, we checked for differences in weight and age between females with the highest and lowest overmarking score in each group. Although these females differed significantly in intrasexual overmarking score ($t_5 = 4.556$, $N = 6$, $P = 0.006$), they were of similar age ($t_5 = -0.530$, $N = 6$, $P = 0.617$) and weight (mean nonpregnant trapped weight; $t_5 = -1.012$, $N = 6$, $P = 0.358$).

Reproductive suppression

Female intrasexual overmarking score does not seem to be a strategy employed to suppress other females. The mean duration of oestrus for females was affected by female age but not by their overmarking score or weight, with older females spending longer in oestrus than younger adult females (Table 3). The number of days a female's onset of oestrus was delayed was not affected by its age (LMM: $\chi^2_1 = 1.94$, $P = 0.163$), weight (LMM: $\chi^2_1 = 0.058$, $P = 0.448$) or intrasexual overmarking score (LMM: $\chi^2_1 = 0.00$, $P = 0.956$), suggesting that all females began oestrus at a similar time but older females remained in oestrus for longer than younger females. When the female with the highest overmarking score in each group was compared to the female with the lowest overmarking score in that group, these females had a similar mean delay in oestrus ($t = 0.233$, $N = 6$, $P = 0.825$; Fig. 5a) and mean duration of oestrus ($t = 0.479$, $N = 6$, $P = 0.652$; Fig. 5b).

Table 3
Linear mixed model on the factors affecting duration of oestrus for individual females

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age	6.75	1	0.015
Weight	1.99	1	0.163
Intrasexual overmarking index	1.17	1	0.286
Minimal model	Coefficient estimate	SE	
Constant	4.188	0.830	
Age	0.001	0.000	

Duration of oestrus was recorded for 34 females in five groups, including 36 group oestrous periods ($N = 206$). 'Group' (estimated variance component = 2.451, SE = 2.440), 'female identity' (estimated variance component = 1.185, SE = 0.777), and 'group oestrus period' (estimated variance component = 3.113, SE = 1.241) were fitted as random terms. Coefficient estimates represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size.

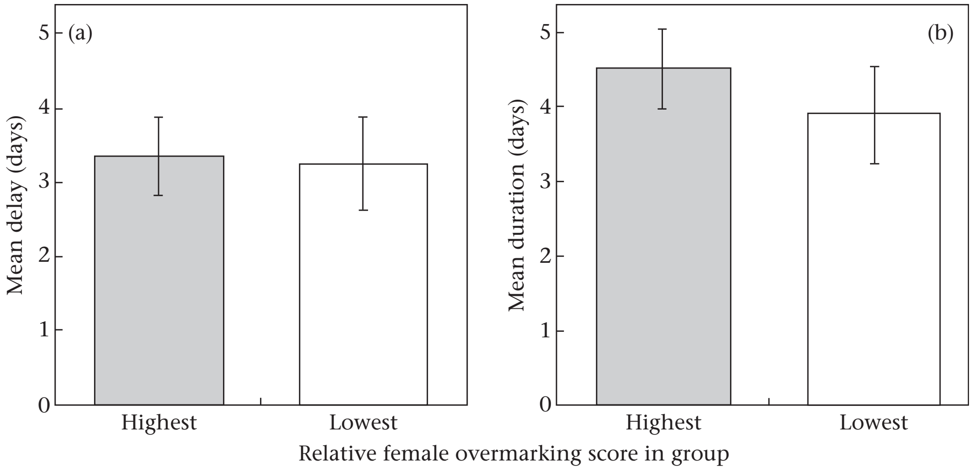

Figure 5. The mean difference ± SE in (a) mean delay in oestrus and (b) mean duration of oestrus for females with the highest and lowest overmarking score in each of six groups. 'Total mean delay' was the mean number of days that each female was first mate-guarded after the first female to be guarded in each oestrous period. 'Total mean duration' was the mean duration for which each female was mate-guarded in each oestrous period.

DISCUSSION

In the Introduction we identified three potential hypotheses that we felt would most likely explain patterns of intrasexual overmarking by females described previously (Jordan et al. 2011a). None of these hypotheses were strongly supported in this study.

In common with previous studies on other species (e.g. common marmoset, *Callithrix jacchus*: Smith et al. 2001; ring-tailed lemur, *Lemur catta*: Palagi & Dapporto 2007; European badger, *Meles meles*: Buesching et al. 2002a, b), anal gland secretions from adult female banded mongooses showed some evidence of individual specificity and stability over time, confirming that female scent marks are likely to be individually recognizable. When all females from the population were included in the same DFA, scents were correctly assigned to the source female significantly more often than expected by chance. However, as we found previously for male scents (Jordan et al. 2011b), incorrect assignments were also common in females. As in males, this may result from reduced selection pressure for high individuality in scents, which is relaxed by the frequent template update opportunities provided by regular repeated exposure to the scents of group members (Jordan et al. 2011b; see Dale et al. 2001).

Intrasexual competition in females may be expected to centre round acquiring or defending resources necessary for successful reproduction (LeBas 2006; Clutton-Brock 2007, 2009; Flower 2007). As females in a poor nutritional state are, perhaps, less likely to reproduce successfully (see Gilchrist et al. 2004), they might be expected to compete intensively for food. However, we found no evidence to suggest that intrasexual overmarking by females was correlated with the likelihood that they would be approached by other individuals in competition for food. Indeed, as we recorded all examples of competition over food resources, the low rates of such competition in banded mongooses suggests that there would be little selection pressure for overmarking to have evolved as a mechanism of resource acquisition in this species. Although it was not possible in this study, it would be informative to investigate differences in overmarking in species where food availability varied either seasonally or spatially. If overmarking were involved in competing for these resources, we might expect more frequent overmarking during periods or sites of intense competition for food, such as seasons of scarcity or in sites of localized but limited abundance. Although scent-marking sites in general are associated with feeding sites in some other species (e.g. African palm civet: Charles-Dominique 1978), it is not known whether these are involved in defence of these sites, and further work is required to tease apart this possibility from the likelihood that scents are 'preferentially' placed there simply because individuals spend more time in those areas.

Females of many species are known to display increased rates of scent marking during their receptive period (e.g. golden hamster: Johnston 1977; klipspringer, *Oreotragus oreotragus*: Roberts & Dunbar 2000), and there is some evidence to suggest that female scents might act as signals of quality, perhaps increasing the likelihood that females will attract and mate with high-quality males (golden hamster: Fischer & Brown 1993). In banded mongooses, highly synchronized oestrous periods (Rood 1975; Cant 2000) may select for elevated female choice. However, we did not find evidence to suggest that females that overmarked more attracted or mated with more males. Although we found some evidence that female intrasexual overmarking score was correlated with the number of mating attempts received from males, levels of harassment received by females during their oestrous period were not affected by their overmarking score. Similarly, the frequency of 'direct' male–male competition for particular females was not related to the female's intrasexual overmarking score. This suggests that males did not preferentially compete for access to females with greater intrasexual overmarking scores. Such incitement of male–male competition by female scent marking has been suggested (see Wolff et al. 2002), but has not yet been shown in mammals. However, as Johnston (2008) pointed out, although overt intrasexual competition is not often apparent (but see ring-tailed lemur 'stink fights': Jolly 1966), female scent marking may still be involved in competition for mates (e.g. Brown 1979). Indeed, we found that females with the highest overmarking score in a group were mate-guarded by males in better condition than the females with the lowest overmarking score (despite these males being of similar ages and weights). This might suggest that females with higher overmarking scores attract and are guarded by males in better condition, which are then more capable of repelling competing males from their vicinity.

Although there is evidence in other species that female scents may reproductively suppress other females (e.g. house mouse: Drickamer 1982), little attention has been paid to the potential that overmarking behaviour might be involved in this process. Although the act of suppressing competitors may be advantageous to the suppressor in many instances, the negative effects on the receiver of encountering these 'primer pheromones' have led some authors to question whether individuals should avoid contact with the scents of competitors (e.g. Drickamer 1986). It has been suggested that female scent marks placed on or in the vicinity of scent marks from other females could help to protect females from primer cues by ensuring that their own scent marks predominate in the environment (Hurst 1990); however, it is perhaps more likely that overmarking, and more generally countermarking, would result in a proliferation of the individual's own cues in the environment. In house mice, urinary scents are very widely distributed, and females do not appear to control their exposure to them (Hurst & Nevison 1994), and so this plethora of cues from multiple individuals appears to provide a mechanism for females to adjust their own reproductive physiology appropriately, according to the current local social conditions and the recipient's own age and social status (Hurst 2005). Indeed, as mongoose scents were almost always investigated by sniffing or licking prior to overmarking, the recipient would be exposed to any such primers if they were present in scent. We found no evidence to suggest that intrasexual overmarking by females was employed as a strategy to suppress other females in banded mongooses. Although urine from grouped female mice delayed first oestrus in others (Drickamer 1982; reviewed in Brown 1985), unfortunately it was not possible to assess any such effect in this study, as female overmarking scores prior to sexual maturity were not available. However, females with high overmarking scores did not seem to delay the oestrus of females with lower overmarking scores within each oestrous period, as the mean duration of a female's oestrous period was not correlated with its overmarking score. Similarly, the females with the highest and lowest intrasexual overmarking scores in each group were mate-guarded for similar durations in each oestrous period. In addition to the mechanistic issues described above, that overmarking did not seem to be involved in female suppression is perhaps not surprising from an adaptive perspective. In banded mongooses, per capita pup survival is greater in mixed litters (Cant et al. 2010), and given that the females most likely to be capable of affording the costs of continual overmarking are probably also more likely to have bigger offspring that can better compete for access to the best helpers (see Hodge et al. 2009), any selective advantage of female suppression may be negligible in this species.

In addition to recognizing the limited data available to test the hypotheses outlined above, we also note that we did not test all potential explanations for the function of intrasexual overmarking by females (see Ferkin & Pierce 2007 for alternative and additional hypotheses). For example, overmarking might allow the formation of a unique group scent, it might be involved in territory defence, or it might function as a bulletin board indicating the presence of individuals in an area. However, none of these hypotheses explains the preference of females to overmark the scents of other females (Jordan et al. 2011a), and this observation, and the considerable frequency with which same-sex scents are overmarked, would certainly not suggest that female intrasexual overmarking has no function at all. Rather, it is possible that overmarking by female mongooses serves multiple functions, and one such function might be developing and maintaining reproductive synchrony within groups, particularly given the benefits of synchronous breeding for pup survival (see Hodge et al. in press). Although there is relatively abundant but debated evidence that scents in general may be involved in synchronizing the reproductive cycles of many species (e.g. human: McClintock 1971; house mouse: Whitten 1956; Jemilio et al. 1986; golden lion tamarin, *Leontopithecus rosalia*: French & Stribley 1987), it is perhaps not immediately clear how female intrasexual overmarking might be involved in reproductive synchrony. However, it is possible that repeated scent marking in one location may allow the constituents of scents responsible for priming individuals to be more effectively discovered by other females, or scents might be concentrated to levels more likely to induce oestrus in other females. The personal observation that individuals, on discovering urine, give recruitment calls is not at odds with this theory, but gathering definitive evidence for the role of scent in synchronization in banded mongooses is a huge challenge and beyond the scope of this particular study. Similarly, it is also not known how long scents, and scent overmarks, persist in the environment; indeed this is unknown for most species (see Buesching & Macdonald 2004). However, scent mark and overmark longevity is unlikely to affect the vast majority of overmarks, as most are placed on scents deposited within that particular observation session and, as groups visit the marking site together as a unit, information on overmarking success should therefore be available to group members during and at the end of each visit.

In conclusion, in this preliminary study of intrasexual female overmarking, we found no evidence to suggest that it is involved in the acquisition and defence of food or suppressing other females. Nor did we find convincing evidence for a role in competition for males. Although we found some evidence suggesting that females with the highest overmarking score were mate-guarded by males in better condition than were females with the lowest overmarking score in each group, these females did not receive more matings or harassment by males than other females. Owing to the relatively low rates of female scent marking in many mammals, but particularly the challenges associated with studying overmarking in the natural environment, the function(s) of scent marking in female mammals remains relatively poorly understood. We suggest that a more thorough theoretical framework should be developed for female overmarking, and more detailed studies of female overmarking should be a research priority, as they represent a conspicuous missing piece in the study of the function(s) of scent marking in general.

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References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **69**, 227–267.

Bro-Jørgensen, J. 2007. Reversed sexual conflict in a promiscuous antelope. *Current Biology*, **17**, 2157–2161.

Brown, R. E. 1979. Mammalian social odours: a critical review. In: *Advances in the Study of Behavior. Vol. 10* (Ed. by J. S. Rosenblatt, R. A. Hinde, C. Beer & M.-C. Busnel), pp. 103–162. New York: Academic Press.

Brown, R. E. 1985. The rodents I: effects of odours on reproductive physiology (primer effects). In: *Social Odours in Mammals. Vol. 1* (Ed. by R. E. Brown & D. W. Macdonald), pp. 245–344. Oxford: Clarendon Press.

Buesching, C. D. & Macdonald, D. W. 2004. Variations in scent-marking behaviour of European badgers *Meles meles* in the vicinity of their setts. *Acta Theriologica*, **49**, 235–246.

Buesching, C. D., Waterhouse, J. S. & Macdonald, D. W. 2002a. Gas-chromatographic analyses of the subcaudal gland secretion of the European badger (*Meles meles*). Part I. Chemical differences related to individual parameters. *Journal of Chemical Ecology*, **28**, 41–56.

Buesching, C. D., Waterhouse, J. S. & Macdonald, D. W. 2002b. Gas-chromatographic analyses of the subcaudal gland secretion of the European badger (*Meles meles*). Part II. Time-related variation in the individual-specific composition. *Journal of Chemical Ecology*, **28**, 57–70.

Cant, M. A. 2000. Social control of reproduction in banded mongooses. *Animal Behaviour*, **59**, 147–158.

Cant, M. A. 2003. Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology*, **259**, 115–121.

Cant, M. A., Hodge, S. J., Bell, M. B. V., Gilchrist, J. S. & Nichols, H. J. 2010. Reproductive control via eviction (but not the threat of eviction) in a cooperative mammal. *Proceedings of the Royal Society B*, **277**, 2219–2226, doi:10.1098/rspb.2009.2097.

Charles-Dominique, P. 1978. Ecology and social behaviour of the African palm civet, *Nandinia biotata*, in Gabon: with a comparison with sympatric prosimians. *Terre et Vie*, **32**, 477–528.

Clutton-Brock, T. H. 2007. Sexual selection in males and females. *Science*, **318**, 1882–1885.

Clutton-Brock, T. H. 2009. Sexual selection in females. *Animal Behaviour*, **77**, 3–11.

Dale, J., Lank, D. B. & Reeve, H. K. 2001. Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *American Naturalist*, **158**, 75–86.

Drickamer, L. C. 1982. Acceleration and delay of first vaginal oestrus in female mice by urinary chemosignals: dose levels and mixing urine treatment sources. *Animal Behaviour*, **30**, 456–460.

Drickamer, L. C. 1986. Puberty-influencing chemosignals in house mice: ecological and evolutionary considerations. In: *Chemical Signals in Vertebrates Vol. IV* (Ed. by D. Duvall, D. Müller-Schwarze & R. M. Silverstein), pp. 441–455. New York: Plenum.

Ferkin, M. H. & Pierce, A. A. 2007. Perspectives on over-marking: is it good to be on top? *Journal of Ethology*, **25**, 107–116.

Fischer, R. B. & Brown, P. S. 1993. Vaginal secretions increase the likelihood of intermale aggression in Syrian hamsters. *Physiology & Behavior*, **54**, 213–214.

Fisher, H. S., Swaisgood, R. R. & Fitch-Snyder, H. 2003. Counter-marking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behavioral Ecology and Sociobiology*, **53**, 425–426.

Flower, T. P. 2007. Competition for food in meerkats (*Suricata suricatta*). M.Sc. thesis, University of Pretoria.

French, J. A. & Stribley, J. A. 1987. Synchronization of ovarian cycles within and between social groups in golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **12**, 469–478.

Gilchrist, J. S. 2004. Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behavioral Ecology*, **15**, 952–960.

Gilchrist, J. S., Otali, E. & Mwanguhya, F. 2004. Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology*, **57**, 119–131.

Gosling, L. M. & Roberts, S. C. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Behavior*, **30**, 169–217.

Heymann, E. W. 2003. Scent marking, paternal care, and sexual selection in callitrichines. In: *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions* (Ed. by C. B. Jones), pp. 305–325. Norman, Oklahoma: American Society of Primatologists.

Hodge, S. J. 2005. Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society B*, **272**, 2479–2484.

Hodge, S. J., Bell, M. B. V., Mwanghuya, F., Kyabulima, S., Waldick, R. & Russell, A. F. 2009. Maternal weight, offspring competition and the evolution of communal breeding. *Behavioral Ecology*, **20**, 729–735.

Hodge, S. J., Bell, M. B. V & Cant, M. A. In press. Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal. *Biology Letters*, doi:10.1098/rsbl.2010.0555.

Hurst, J. L. 1990. Urine marking in populations of wild house mice *Mus domesticus* Rutty. II. Communication between females. *Animal Behaviour*, **40**, 223–232.

Hurst, J. L. 2005. Scent marking and social communication. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 219–243. Cambridge: Cambridge University Press.

Hurst, J. L. & Nevison, C. M. 1994. Do female house mice, *Mus domesticus*, regulate their exposure to reproductive priming pheromones? *Animal Behaviour*, **48**, 945–959.

Jemilio, B., Harvey, S. & Novotny, M. 1986. Promotion of the Whitten effect in female mice by synthetic analogs of male urinary constituents. *Proceedings of the National Academy of Sciences, U.S.A.*, **83**, 4576–4579.

Johnston, R. E. 1977. The causation of two scent-marking behaviour patterns in female hamsters (*Mesocricetus auratus*). *Animal Behaviour*, **25**, 317–328.

Johnston, R. E. 2005. Eavesdropping and scent over-marking. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 344–372. Cambridge: Cambridge University Press.

Johnston, R. E. 2008. Individual odors and social communication: individual recognition, kin recognition, and scent over-marking. *Advances in the Study of Behavior*, **38**, 439–505.

Johnston, R. E. & Bhorade, A. 1998. Perception of over-marks: novel mechanisms for determining which individual's mark is on top. *Journal of Comparative Psychology*, **112**, 230–243.

Johnston, R. E., Chaing, G. & Tung, C. 1994. The information in scent over-marks of golden hamsters. *Animal Behaviour*, **48**, 323–330.

Johnston, R. E., Munver, R. & Tung, C. 1995. Scent counter marks: selective memory for the top scent by golden hamsters. *Animal Behaviour*, **49**, 1435–1442.

Johnston, R. E., Sorokin, E. S. & Ferkin, M. H. 1997. Female voles discriminate males' over-marks and prefer top-scent males. *Animal Behaviour*, **54**, 679–690.

Jolly, A. 1966. *Lemur Behavior.* Chicago: University of Chicago Press.

Jordan, N. R. 2007. Scent-marking investment is determined by sex and breeding status in wild meerkats. *Animal Behaviour*, **74**, 531–540.

Jordan, N. R., Mwanguhya, F., Kyabulima, S., Rüedi, P. & Cant, M. A. 2010. Scent marking within and between groups of wild banded mongooses. *Journal of Zoology*, **280**, 72–83.

Jordan, N. R., Manser, M. B., Mwanguhya, F., Kyabulima, S., Rüedi, P. & Cant, M. A. 2011a. Scent marking in wild banded mongooses: 1. Sex-specific scents and overmarking. *Animal Behaviour*, **81**, 31–42.

Jordan, N. R., Mwanguhya, F., Furrer, R. D., Kyabulima, S., Rüedi, P. & Cant, M. A. 2011b. Scent marking in wild banded mongooses: 2. Intrasexual overmarking and competition between males, *Animal Behaviour*, **81**, 43–50.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. *Educational and Psychological Measurement*, **20**, 141–151.

Kvarnemo, C., Moore, G. I. & Jones, A. G. 2007. Sexually selected females in the monogamous Western Australian seahorse. *Proceedings of the Royal Society B*, **274**, 521–525.

Lacher, T. E. Jr., Da Fonseca, G. A. B., Alves, C. Jr. & Magalháes-Castro, B. 1981. Exudate-eating, scent-marking, and territoriality in wild populations of marmosets. *Animal Behaviour*, **29**, 306–307.

LeBas, N. R. 2006. Female finery is not for males. *Trends in Ecology & Evolution*, **21**, 170–173.

McClintock, M. K. 1971. Menstrual synchrony and suppression. *Nature*, **229**, 244–245.

Macdonald, D. W. 1978. Observations on the behaviour and ecology of the striped hyena, *Hyaena hyaena*, in Israel. *Israel Journal of Zoology*, **27**, 189–198.

Massey, A. & Vandenbergh, J. B. 1980. Puberty delay by a urinary cue from female house mice in feral populations. *Science*, **209**, 821–822.

Massey, A. & Vandenbergh, J. G. 1981. Puberty acceleration by a urinary cue from male mice in feral populations. *Biology of Reproduction*, **24**, 523–525.

Mousseau, T. A. & Fox, C. W. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, **13**, 403–407.

Müller, C. A. & Manser, M. B. 2008a. Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology*, **114**, 174–185.

Müller, C. A. & Manser, M. B. 2008b. Mutual recognition of pups and providers in the cooperatively breeding banded mongoose. *Animal Behaviour*, **75**, 1683–1692.

Palagi, E. & Dapporto, L. 2007. Females do it better. Individual recognition experiments reveal sexual dimorphism in *Lemur catta* (Linnaeus 1758) olfactory motivation and territorial defence. *Journal of Experimental Biology*, **210**, 2700–2705.

R Development Core Team. 2008. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. http://www.R-project.org.

Ralls, K. 1971. Mammalian scent marking. *Science*, **171**, 443–449.

Rich, T. J. & Hurst, J. L. 1998. Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour*, **56**, 727–735.

Rich, T. J. & Hurst, J. L. 1999. The competing countermarks hypothesis: reliable assessment of competitive ability by potential mates. *Animal Behaviour*, **58**, 1027–1037.

Roberts, S. C. & Dunbar, R. I. M. 2000. Female territoriality and the function of scent-marking in a monogamous antelope (*Oreotragus oreotragus*). *Behavioral Ecology and Sociobiology*, **47**, 417–423.

Rood, J. P. 1974. Banded mongoose males guard young. *Nature*, **248**, 176.

Rood, J. P. 1975. Population dynamics and food habits of the banded mongoose. *East African Wildlife Journal*, **13**, 89–111.

Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., McIlrath, G. M., Dalerum, F. D., Cameron, E. Z. & Barnard, J. A. 2002. Factors affecting pup growth and survival in cooperatively breeding meerkats *Suricata suricatta*. *Journal of Animal Ecology*, **71**, 700–709.

Rylands, A. B. 1985. Tree-gouging and scent-marking by marmosets. *Animal Behaviour*, **33**, 1365–1367.

Schall, R. 1991. Estimation in generalized linear models with random effects. *Biometrika*, **78**, 719–727.

Smith, T. E., Tomlinson, A. J., Mlotkiewicz, J. A. & Abbott, D. H. 2001. Female marmoset monkeys (*Callithrix jacchus*) can be identified from the chemical composition of their scent marks. *Chemical Senses*, **26**, 449–458.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine-Atherton.

Whitten, W. K. 1956. Modification of the oestrous cycle of the mouse by external stimuli associated with the male. *Journal of Endocrinology*, **13**, 399–404.

Wolff, J. O., Mech, S. G. & Thomas, S. A. 2002. Scent marking in female prairie voles: a test of alternative hypotheses. *Ethology*, **108**, 483–494.

APPENDIX

Table A1
Definition of terms used in analyses

Term	Description	Relevant hypothesis
Relative foraging challenges	Observed minus expected foraging challenges per female = (foraging challenges directed at particular female/foraging challenges directed towards all females in group[*])–(1/females in group[*])	Resource acquisition
Harassment	Measure of males within 2m during oestrus = (mean adult males <2m)–(adult males/oestrous females) Calculated for each oestrous female with >9 scans in each oestrous session	Mating competition
Relative male–male competition	(male–male competition over particular female/total male–male competition in group)–(1/females in group[*])	
Mean delay in oestrus[†]	Mean number of days female was initially mate-guarded after the first female in group was mate-guarded. Females that were not mate-guarded in a given oestrous period were given a delay score equal to the total length of the oestrous period	Reproductive suppression
Mean duration of oestrus[†]	Females that were not mate-guarded in a given oestrous period were given a duration of zero for that period	

[*] Only females that were adult at the start of the study and survived beyond the date at which the last competition data were collected at that group were included, to ensure they had equal opportunity to be competed with/over.

[†] These measures only included group oestrous periods where at least two females were mate-guarded, and females were only included in analyses if they were mate-guarded in two or more periods.

Table A2
General linear mixed model on the factors affecting competition with females over food by adult females only

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age	1.21	19	0.242
Weight	−0.56	19	0.581
Intrasexual overmarking score	0.71	19	0.488
Minimal model	Coefficient estimate	SE	
Constant	−0.0003	0.004	

Data from 23 females were fitted to a general linear regression.

Table A3
General linear mixed model on the factors affecting competition with females over food by adult males only

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age	−0.26	10	0.242
Weight	−0.69	10	0.507
Intrasexual overmarking score	−0.03	10	0.980
Minimal model	Coefficient estimate	SE	
Constant	−0.001	0.001	

Data from 14 females were fitted to a general linear regression.

Table A4
General linear mixed model on the factors affecting competition with females over food by adult males and females combined

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age	1.00	21	0.330
Weight	0.86	21	0.398
Intrasexual overmarking score	0.17	21	0.865
Minimal model	Coefficient estimate	SE	
Constant	−0.001	0.001	

Data from 25 females were fitted to a general linear regression.