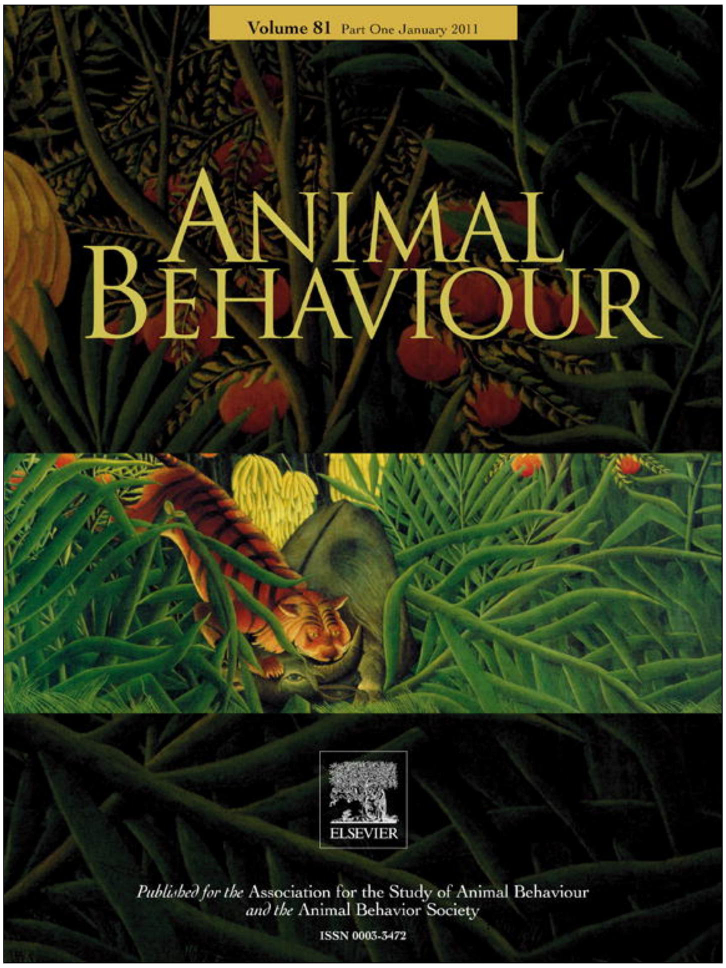
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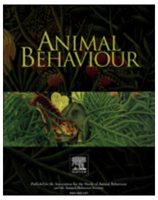

Scent marking in wild banded mongooses: 1. Sex-specific scents and overmarking

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Overmarking occurs when one individual places its scent mark directly on top of the scent mark of another individual. Although it is almost ubiquitous among terrestrial mammals, we know little about the function of overmarking and detailed field observations are rare. We investigated the chemical composition of scents and patterns of overmarking by wild banded mongooses, *Mungos mungo*. Chemical analyses of anal gland secretions showed that scents were sexually dimorphic. Both male and female adults were more likely to overmark the scents of same-sex individuals. An analysis of responses to two scents on the same site suggested that the sex of the top or most recent scent was more important than that of the bottom or original scent in determining overmarking response. Juveniles also overmarked scents at high rates, but did not respond to scents in a sex-specific way. Same-sex-specific patterns within groups have not been described in any other species, and may reflect a social system with intense intrasexual competition for reproduction within both sexes. Banded mongooses live in large mixed-sex groups, with intense competition between males for females, owing to the heavily male-biased adult sex ratio and highly synchronized oestrous cycles. Oestrous synchronization may also promote intrasexual competition for males within females, as females compete simultaneously for high-quality males. Female competition for males may also be enhanced by the rewards of male-biased parental care. This investigation highlights the need for detailed studies of overmarking in the natural context, to confirm and expand upon laboratory findings.

In mammals, the importance of scent in regulating territorial spacing is well established, and scent marks are commonly deposited in locations that appear to maximize the chance of intercepting territorial intruders, such as along territorial borders (e.g. European badger, *Meles meles*: Kruuk 1978; oribi, *Ourebia ourebi*: Brashares & Arcese 1999a, b; Eurasian beaver, *Castor fiber*: Rosell et al. 1998), at trail crossroads (e.g. Iberian wolf, *Canis lupus*: Barja et al. 2004) or concentrated around key resources within territories (Gorman & Mills 1984; Mills & Gorman 1987). However, owing to the difficulties of directly observing wild animals, previous studies have tended to focus on the spatial distribution of visually conspicuous scent signals such as scats (e.g. Roper et al. 1993; Barja et al. 2004; but see Gorman 1980 for exceptions). Consequently, relatively little is known about individual contributions to scent marking, particularly with glandular secretions (but see Brotherton 1994; Stewart et al. 2002; Buesching & Macdonald 2004). To understand fully the function(s) of scent marking we need to consider not only the broad spatial patterns of scent deposition, but also both the information content of olfactory signals and the response of individuals to scent marks in the natural context.

An apparently common response to encountered scent marks is ‘overmarking’. Overmarking occurs when one individual places its scent mark directly on top of the scent mark of another individual (Johnston et al. 1994), and anecdotal observations suggest that overmarking is widespread in many mammals (e.g. grey wolf, *C. lupus*: Rothman & Mech 1979; plains zebra, *Equus burchelli*: Klingel 1967; reviewed in Ferkin & Pierce 2007). Overmarking occurs

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within breeding pairs, in which males typically scent mark on top of the scents of their mates (e.g. meerkat, *Suricata suricatta*: Jordan 2007; Kirk's dik-dik, *Madoqua kirkii*: Brotherton 1994; grey wolf: Peters & Mech 1975; pronghorn, *Antilocapra americana*: Moodie & Byers 1989), and in other species individuals are known to overmark the scents of same-sex individuals (e.g. equids: Linklater 2000). Such intrasexual overmarking is often interpreted as a form of intrasexual competition, as only individuals in good condition may be able to afford the costs of continually overmarking their rivals' scent (i.e. the 'competing countermarks hypothesis', Rich & Hurst 1998, 1999). However, it remains unclear how common or important overmarking is in the natural environment, and whether the patterns observed in a small number of species in captivity are replicated in the same and other species in the wild.

Banded mongooses, *Mungos mungo*, offer an opportunity to study overmarking in the natural context, as they live in constant close proximity to both reproductive rivals and potential mates within cohesive social groups (see Cant 2000). These large mixed-sex groups (8–70 individuals) contain no clear dominant pair; instead, groups are made up of a core of breeding adult males (2–15 males/group) and multiple (1–8) breeding females (Rood 1975; Cant 2000; Cant et al. 2010). Within groups, males compete intensively with male relatives for mating opportunities with close female relatives during highly synchronized oestrous periods (Cant 2000). Previous presentation experiments using urine and scats from other groups suggested that mongooses were more likely to overmark the scents of same-sex individuals, supporting the idea that scents may be important in intrasexual competition in this species (Müller & Manser 2008a). However, intrasexual competition for reproduction is likely to be most intense within social groups in this species, as immigration into existing stable social groups almost never occurs (only two individuals joined an existing pack in 11+ years of observation; Bell 2006), and most successful mating occurs within social groups (unpublished data; but see Cant et al. 2002). Previous work on the broad spatial distribution of scent marks within territories suggests that scents are not preferentially placed in border regions, but are distributed throughout the home range (Jordan et al. 2010). This is consistent with the notion that scents may be important for intragroup communication, in addition to their established role in territorial defence (Müller & Manser 2007, 2008a; Jordan et al. 2010). As yet, detailed patterns of overmarking have not been described.

We investigated potential sex differences in the chemical composition of scents and in patterns of overmarking in response to naturally encountered scent marks and scent overmarks in wild banded mongooses. Here we discuss these results in relation to possible functions of overmarking in this species. If overmarking is involved in intrasexual competition for mates or mating opportunities, we might expect individuals to concentrate their overmarking effort on scent marks produced by members of the same sex. To allow sex discrimination of scents by potential overmarkers, we might also predict sex differences in scent composition, although this is not a prerequisite. Alternatively, if overmarking is involved in competition for resources other than mates, such as food, it might be expected that males and females overmark indiscriminately with regard to sex, as both sexes share a similar diet and do not differ in their utilization of other nonmating resources. Finally, if scent marking has different functions within and between groups we might expect patterns of overmarking to be affected by their location in the home range. For example, intrasexual competition for mates might be most important in exclusive regions of the range, where reproductive rivals are encountered, whereas territory defence may be more important in areas of the home range that overlap. If this were the case we might expect sex-biased overmarking to be more common in exclusive regions, and for scents to be placed independently in areas of overlap with other groups.

METHODS

Study Site, Population and Identification

Data were collected from December 2005 to November 2007 from nine wild groups of habituated, individually identifiable, banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E). The habitat is medium-height grassland (principally *Sporobolus pyramidalis* and *Chloris* spp.) dotted with *Euphorbia candelabrum* trees and thickets of *Capparis tomentosa* and *Azima tetracantha* (Spinage 1982). Annual rainfall is typically 800–900 mm, with two dry periods in January–February and June–July each year (Rood 1975; for further details of the study area see Cant 2000). Mean adult group size was 16.6 adults with a pronounced sex bias of 2.25 adult males per adult female (Jordan et al. 2010).

All individuals were uniquely marked with an identifying hair-clip to the fur, or a coloured plastic collar which was renewed during routine trapping events (see Jordan et al. 2010 for full details), and one individual in each group was fitted with a radio-collar. Individuals were trapped in box traps baited with leftovers from local restaurants. Traps were set in the shade in the early morning and, to minimize the mongooses' time in the traps and potential vulnerability to predators, were monitored at least every hour, but commonly observers sat at a distance observing through binoculars. No evidence of predators approaching traps was recorded during the study. Where specific individuals were targeted, an observer sat about 15 m from a baited trap and released a string to trigger the trap when the target individual entered. When individuals had been captured, traps were removed and replacements were monitored while other observers processed the first batch. Traps containing mongooses were covered with a cloth and driven to the laboratory on the back of a pick-up truck (maximum distance ca.4 km). Individuals were coaxed from the traps into a black cloth bag tied around the entrance, and a mask delivering isoflurane was placed over the muzzle through the cloth. To allow long-term identification of each individual, a tattoo of the group code and individual number were applied to the inner thighs of all individuals during their first capture. Additionally, for rapid identification in the field individuals were given a unique haircut (e.g. shoulder region, tail-base region, etc.) and/or fitted with a coloured plastic collar. To ensure that the collar could move freely, an index finger was inserted between the mongoose's neck and the collar before tightening. One individual in each group was fitted with a Sirtrack radiocollar (Sirtrack, Havelock North, New Zealand) weighing 22.85 ± 3.11 g (mean ± SD; range 17–28 g), which is 1.46% of the body mass (range 0.95–1.87%). Radiocollars were fitted following identical collaring procedures outlined for meerkats (Golabek et al. 2008), and located using Telonics TR-4 receivers (Telonics Inc., Mesa, AZ, U.S.A.) from up to 1 km. No mongooses died or aborted fetuses as a result of trapping conducted for this study. To allow recovery, individuals were placed back into the trap and their breathing rates monitored until they regained normal locomotory ability, usually between 1 and 7 min. The traps were then covered and individuals were released back to their group together (after the last individual had been processed and recovered) within 4 h of having been captured. Two individuals stopped breathing during anaesthesia and were successfully revived by gently blowing air into their lungs through a clenched fist clasped over their muzzle. Bait remains were left in the traps throughout the procedure, and water was initially provided by clipping hamster bottles to the trap side on their arrival at the laboratory. Although the mongooses readily drink from these bottles during weighing sessions in the field, the first 42 individuals trapped did not drink in the laboratory and so water provision was abandoned from then on.

The research was cleared by the Ethical Committee of the Department of Zoology at the University of Cambridge and undertaken under permit from the Uganda Wildlife Authority (UWA), and the Uganda National Council for Science and Technology. Samples were exported under UWA material transfer agreements and imported into Switzerland under licences from the Swiss Federal Veterinary Office.

Individuals were followed from first emergence from the den, and their birth dates were accurately recorded by monitoring the weight (and shape) change of pregnant females. Individuals were classified as adults when they reached 365 days old, and were juveniles up to 290 days which is the youngest age at which females were known to conceive (Cant 2000). Banded mongooses deposit scent from five distinct sources: anal marks are deposited by dragging the anal region across a horizontal object or surface; cheek marks involve rubbing the side of the 'face' on horizontal or vertical objects and the ground; token urination is distinguished from simple urination as it involves a stereotyped stamping of the hindlegs; and scats are deposited in token amounts at specific marking sites called latrines (Jordan et al. 2010).

Scent Collection and Composition Analysis

Scent sampling and scent storage procedures are described in full detail elsewhere (Jordan et al. 2010). During anaesthesia (described above and in Jordan et al. 2010), anal gland secretions (AGS) were exuded directly from the gland into cleaned glass vials (Chromacol, Welwyn Garden City, U.K.) with PTFE-faced cap and septa (Chromacol, Welwyn Garden City, U.K.). Vials were immediately frozen in liquid nitrogen and remained there until they were transported back to Europe in a dryshipper (International Cryogenics Inc., Indianapolis, IN, U.S.A.). Eighty adult mongooses (40 males, 40 females) were sampled from eight stable social groups between December 2005 and April 2006.

Chemical profiles for AGS samples were obtained by gas chromatography–mass spectrometry (GCMS) using a Hewlett-Packard 5890 Series II gas chromatograph (GC) fitted with an HP-5 column (25 m × 0.2 mm internal diameter × 0.33 μl) and coupled to a Hewlett-Packard 5971 Series Mass Selective Detector (mass spectrometer; MS). Samples were removed from a storage freezer at −80 °C in batches on the day of analysis, and held in the laboratory on dry ice during this period (−78.5 °C). Vials were taken individually from dry ice and a few drops of the sample were removed using a stainless steel spatula and immediately added to a reagent tube containing 1 ml of solvent (MTBE; methyl tert-butyl ether, 99.8% HPLC grade, Fluka Chemie, Buchs, Switzerland) and 10 μl of dichloromethane (analysis grade). Samples were vigorously mixed on a vortex mixer (30 s) before being filtered through medicinal cotton wrapped over the edge of a glass pipette. Samples were run overnight with an HP 6890 series injector controlled by an HP GC AutoSampler; 1 μl of the dissolved sample/solvent mixture was automatically injected directly into the column which had a solvent delay of 2 min, and a start temperature of 50 °C, increasing by 8 °C/min to 240 °C, where it remained for a further 10 min. Between each sample, the GC was heated to 280 °C for 5 min, and after every seven samples a 'blank' was run to ensure that no contamination was left in the column. Blanks consisted of the solvent mixture filtered through medicinal cotton. Results were automatically saved (HP G1030 MS ChemStation V.B. 00.01. software) and, where possible, compounds were tentatively identified by a combination of their retention times and mass spectra (using the Wiley138 chemical database). As we were primarily interested in broad differences in scent profiles across social categories, we did not validate compound identification with pure compounds.

Behavioural Observations

Scent marking and overmarking events were recorded by critical incident sampling (Altmann 1974), and overmarking was defined as the placement of a scent mark on an existing scent mark produced by another individual, so that the two scents were at least partially overlapping (sensu Johnston et al. 1994). When the first individual was seen to scent mark a location, the scent mark type, the substrate marked and the identity of the individual that scent marked were recorded. Each 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 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. Coordinates of all scent marks observed to be deposited were recorded on handheld Garmin 12 Global Positioning System (GPS) units, and a subsample of original scent marks (i.e. first scent mark at a particular scent station) was used to determine whether particular substrates were preferentially marked with different scent types or by the different sexes. The first mark at a site was termed the 'original mark' and the most recent overmark on a scent station was termed the 'top mark'. The locations of scent marks were plotted on home range maps and categorized as occurring in areas of intergroup overlap or exclusive use. Home range analyses were conducted following procedures outlined previously (Jordan et al. 2010), and areas of overlap were calculated within the 95% kernel. To determine the factors affecting whether or not an encountered scent would be overmarked, we analysed the probability that an individual overmarked a scent that it investigated (sniffed or licked). Only overmarks following investigation were included in analyses. However, although the 'original' mark was the first to be deposited in a scent station during an observation session, it was not necessarily the first ever, as scent stations may have been visited in periods prior to the current observation session.

To determine the relative importance of top versus bottom ('original') scents in determining an investigating individual's overmarking response, we considered all encounters with double scent marks in a separate analysis. Encounters with double scent marks occurred when an individual investigated a scent station that had previously been marked twice, once each by two other individuals. Unfortunately, models including 'top mark type' and 'bottom mark type' as explanatory variables failed to converge, owing to the large number of variables and factor levels. Therefore, as mark type was not of interest per se but needed to be accounted for, we ran models using only the data for which the top mark type was the same as the initial mark type, and included mark type as a variable.

Statistical Analyses

Scent mark composition

Chemical data were analysed in SPSS 15.0 (SPSS Inc., Chicago, IL, U.S.A.). Principal component analysis (PCA) was conducted to reduce the dimensionality of log percentage abundances of 35 eluted compounds detected by GCMS, and to ensure the independence of variables for subsequent analyses. These principal components were extracted using the Kaiser method (Kaiser 1960), and subsequently entered into a discriminant function analysis (DFA). DFA identifies linear combinations of these principal components and assigns each sample to its appropriate category (correct assignment) or to another category (incorrect assignment).

For external validation we used a leave-one-out cross-validation procedure, and to fulfil the requirements of independence (Mundry & Sommer 2007) we randomly chose only one sample per individual. Post hoc 'bootstrapping' analyses were conducted in 'R' (R Development Core Team 2008) 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

Behavioural data were analysed using Genstat Release 10.1 (Lawes Agricultural Trust, Rothamsted, U.K.). We constructed binomial generalized linear mixed models (GLMMs) with a logit-link function, and fitted overmarking response as the response variable ($1 = $ overmarked, $0 = $ not overmarked), with a binomial total of 1. We conducted separate analyses for juvenile and adult investigators, but fitted 'group', 'scent station', 'investigator ID' and 'encountered scent ID' as random factors in all analyses to account for repeated measures. Home range region (exclusive/overlap) was included as a random factor in all presented models.

RESULTS

Scent Mark Composition

The first seven principal components derived from anal gland secretions of 80 adult mongooses (40 males, 40 females) from eight stable social groups explained 75.8% of the variance in the data. Of the 80 samples, 73 (91.3%) were correctly assigned to the correct sex, compared to 50% expected by chance (bootstrapping; $P = 0.029$). Chromatograms showed distinct consistent visual differences between the sexes (see Appendix Fig. A1), and DF scores for samples showed clear sex specificity (Fig. 1).

Behavioural Observations

Encountered single scents

Whether a single scent mark was overmarked by an investigating animal was significantly affected by an interaction between the sex of the investigator and that of the original marker; males and females were significantly more likely to overmark scent marks deposited by same-sex individuals (see Appendix Table A1). This result is not explained by individuals potentially encountering more scents from members of their own sex, as this possibility was accounted for in the model. Additionally, males and females were similarly likely to initiate marking bouts on different substrate types (ground, object, shrub/twig, dung, concrete; chi-square goodness-of-fit test: $\chi^2_4 = 5.385$, $N = 464$, $P = 0.250$; Table 1), ruling out the possibility that individuals coincidentally overmark same-sex scents by a potential sex preference for specific sites. Additionally, the original mark type affected the likelihood of overmarking, through significant interactions with the sex of the investigator and the sex of the original marker (see Appendix Table A1). However, as we were primarily interested in the sex-specific response of individuals to scent marks, and not the response to different scent types per se, further analyses were performed on the response of individuals to encountered single scents of each type separately. As Table A2 in the Appendix shows for token urination marks, overmarking was affected by the interaction between the sex of the original marker and the investigator; again, males were significantly more likely to overmark a single scent mark deposited by another male than by another female, whereas females were significantly more likely to overmark single scent marks of other females. This interaction (between the sex of the original marker and the sex of the investigator) was significant for all scent mark types (GLMM: anal: $\chi^2_1 = 7.85$, $N = 343$, $P = 0.005$; urine: $\chi^2_1 = 29.33$, $N = 232$, $P < 0.001$; scat: $\chi^2_1 = 9.36$, $N = 626$, $P = 0.002$), except cheek marks which yielded insufficient data to assess this.

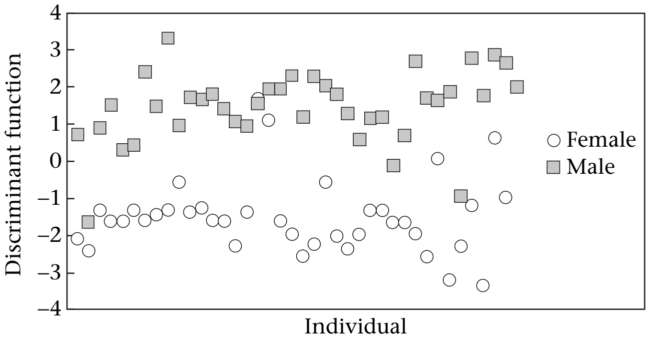

Figure 1. Plot of discriminant function scores for anal gland secretions collected from 80 adult banded mongooses (40 females: ▨; 40 males: ○). Each individual contributed only one scent sample to the data set (December 2005–April 2006). DFA was performed on seven principal components generated by PCA (correlation matrix) on log-transformed percentage abundances (percentage of total compounds eluted from 10–37 min) of 35 distinct compounds eluted during GCMS analyses.

Encountered double scents

The overmarking response to encountered double scents was affected by scent mark type and an interaction between 'top mark sex' and 'investigator sex' (see Appendix Table A3). Original marker sex did not have a significant effect on the likelihood that an investigator would overmark the encountered scent station (see Appendix Table A3).

All encountered scents

As incorporation of too many variables resulted in nonconvergence of models, and a previous result (above) showed that overmarking response was affected by characteristics of the most recent scent mark, and not the bottom scent mark, factors pertaining to the bottom scent were excluded from analyses of more complex mark sites. Again, encountered scent mark type had a significant effect on overmarking for both adults and juveniles (see Appendix Table A4). In both cases glandular marks were proportionately more likely to be overmarked than nonglandular scent types (token urine/urine/scats; see Appendix Fig. A2), and to simplify interpretation we conducted further analyses on each scent type separately.

Adult individuals were significantly more likely to overmark scent marks from members of the same sex for all mark types except cheek marks (Appendix Table A5, Fig. 2). Females were more likely to overmark urine (and token urine) from opposite-sex individuals than were males, but there was no difference in other scent types (Fig. 2). In contrast to adults, the probability that a juvenile would overmark an encountered scent mark was not affected by an interaction between its sex and the sex of the scent it encountered (GLMM: $\chi^2_1 = 0.08$, $N = 203$, $P = 0.776$). Instead, scent mark type was the only factor affecting overmarking in juveniles (see Appendix Table A4).

Age affected the probability of overmarking encountered same-sex scent marks. Across the entire data set, older individuals were more likely to overmark scents from same-sex individuals than younger adult individuals (see Appendix Fig. A3a). This relationship with age appears to be caused by a strong effect during sexual maturity (see Appendix Fig. A3b), and age did not affect overmarking by adult (>365 days) individuals (see Appendix Fig. A3c).

DISCUSSION

Anal gland secretions of adult banded mongooses are sexually dimorphic, and adults were more likely to overmark the scent of

Table 1
Percentage of scent marks of five types deposited on different substrates by adult mongooses

	Anal		Token urine		Urine		Scat		Cheek		Total	
	F	M	F	M	F	M	F	M	F	M	F	M
	(12)	(56)	(60)	(133)	(18)	(16)	(68)	(96)	(3)	(2)	(161)	(303)
Substrate												
Ground	41.7	37.5	70.0	56.4	88.9	81.3	92.6	90.6	0.0	0.0	78.3	64.7
Object	16.7	26.8	16.7	12.8	0.0	6.3	1.5	3.1	33.3	0.0	8.7	11.9
Shrub/twig	33.3	25.0	6.7	10.5	5.6	0.0	1.5	1.0	33.3	50.0	6.8	9.9
Dung	8.3	8.9	1.7	9.8	5.6	12.5	1.5	5.2	33.3	0.0	3.1	8.3
Concrete	0.0	1.8	5.0	10.5	0.0	0.0	2.9	0.0	0.0	50.0	3.1	5.3

F: female; M: male. Sample sizes are given in parentheses.

same-sex individuals than of opposite-sex individuals within their own social group. This result was similar for single scent marks and for scent stations containing multiple marks, and an evaluation of the encounters with double scent marks suggested that factors pertaining to the top scent mark were more important than the original scent mark in determining overmarking response. In contrast to adults, juveniles did not respond to adult scents in a sex-specific way, with the proportion of encountered same-sex scents that were overmarked increasing during maturity. Finally, mongooses were more likely to overmark encountered glandular secretions than they were excretory scents.

Sex-specific anal gland secretions in banded mongooses may reflect the importance of remote discrimination between the sexes. Many other species show sex differences in glandular secretions (e.g. *Microtus* spp.: Ferkin 2001; Egyptian mongoose, *Herpestes ichneumon*: Hefetz et al. 1984; European rabbit, *Oryctolagus*

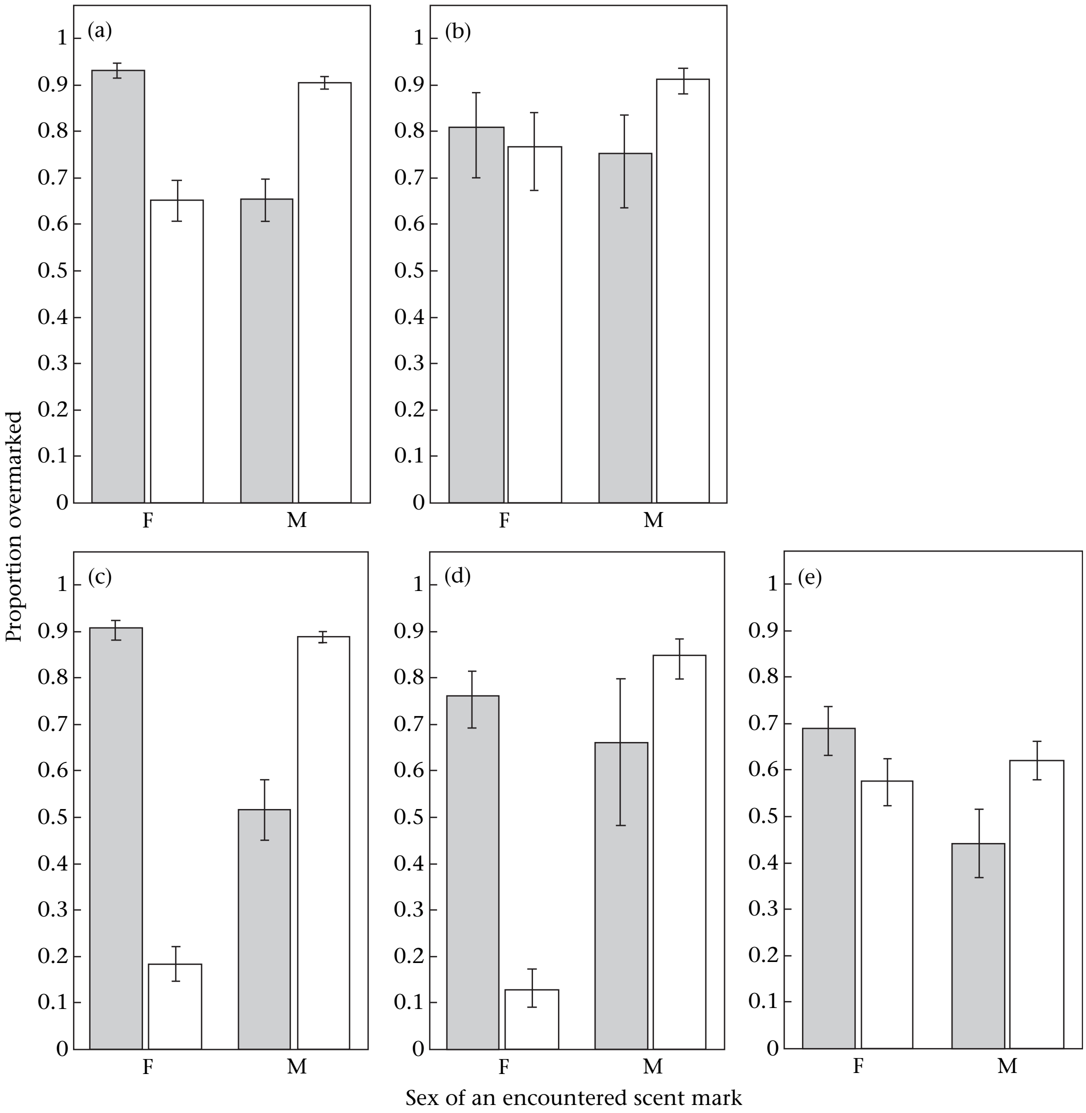

Figure 2. The effect of the interaction between the sex of the individual depositing an encountered scent mark and the sex of the investigator on overmarking of five encountered mark types deposited and investigated by adults: (a) anal, (b) cheek, (c) token urination, (d) urination and (e) scat. Grey bars: female investigator; white bars: male investigator. F: female scent mark; M: male scent mark. Means ± SEs are shown and were generated from predicted means of the GLMMs presented in Appendix Table A4.

cuniculus: Goodrich & Mykytowycz 1972). Sex discrimination via olfactory cues appears to be a common phenomenon (e.g. ferret, *Mustela putorius furo*: Cloe et al. 2004; spotted hyaena, *Crocuta crocuta*: Drea et al. 2002; meadow vole, *Microtus pennsylvanicus*: Ferkin & Johnston 1995, Ferkin 1999a, b), and sexually specific information in scents may be used in many contexts, including territorial and mating behaviour.

Same-sex, or intrasexual, overmarking is common in the territorial context in many mammal species, presumably as intruders represent a greater threat to same-sex residents (e.g. banded mongooses: Müller & Manser 2008a). In other species, overmarking seems to be common within social groups, where it commonly involves males overmarking females (e.g. grey wolf: Peters & Mech 1975; meerkat: Jordan 2007), and has been interpreted as a signal of 'ownership' or an advertisement of a male's commitment to defend females (e.g. European badger: Roper et al. 1986; meerkat: Jordan 2007). In contrast to these studies, we found that adult banded mongooses were more likely to overmark the scents of same-sex individuals within their own group. Scent marking in response to same-sex scents has been documented in a number of species, including golden hamsters, *Mesocricetus auratus* (Johnston 1977) and bank voles, *Clethrionomys glareolus* (Rozenfeld & Denoël 1994), but these cases did not involve direct overmarking, in contrast to what we have described here for banded mongooses. In fact, evidence from prairie voles, *Microtus ochrogaster*, and meadow voles suggests that deliberate deposition of scents as overmarks may not occur in these species at least (Thomas & Wolff 2002), despite evidence of specialized mechanisms for deriving information from overmarks obtained by experimentation in the same species (e.g. Ferkin et al. 2001, 2005) and in golden hamsters (Wilcox & Johnston 1995; Johnston & Bhorade 1998). In common with such studies (e.g. golden hamsters: Johnston et al. 1994; Johnston & Bhorade 1998; meadow voles: Johnston et al. 1997), we found evidence to suggest that individuals perceived the top scent as of increased importance relative to the bottom scent in a double scent mark. We found that an individual's responses to double scent marks were affected by an interaction between its own sex and the sex of the top scent marker and not by the bottom scent. While this does not demonstrate a masking effect of the bottom scent by the top scent, as had been suggested previously for golden hamsters (Johnston et al. 1994), it does at least suggest that the top mark is assigned 'greater significance' over the previous mark by virtue of its position, as experiments with partially overlapping scents suggest in some rodents (e.g. Johnston et al. 1995; Wilcox & Johnston 1995). Whether, as in golden hamsters (Johnston et al. 1994) and meadow voles (Johnston et al. 1997), individuals prefer subsequently to associate with opposite-sex individuals whose marks are on top is not yet known in banded mongooses, but these results support the hypothesis that overmarking is involved in intrasexual competition, and build upon intergroup experiments which stimulated a similarly sex-specific overmarking response (Müller & Manser 2008a).

In contrast to most social groups of mammals, where reproductive rivals are principally found outside the territory, competition for reproductive opportunities occurs primarily within banded mongoose groups. Only one in 267 successful matings occurred with individuals from outside their own social group during the study period (unpublished data; but see Cant et al. 2002), and because of synchronous oestrus in females, and a high adult male:female sex ratio, males in particular exhibit intense intrasexual competition for access to receptive females (Cant 2000). Intrasexual overmarking in males as observed in this study may therefore be consistent with a function in intrasexual competition, as only high-quality males may be able to afford the distribution costs of overmarking the scents of rivals (e.g. Rich & Hurst 1998, 1999). As such, females might be expected to base mate choice decisions on the frequency of overmarking (Ferkin et al. 2005), and this idea is supported by evidence from captive studies. Female meadow voles, when presented with experimental overmarks, subsequently preferred to associate with the male whose mark was on top (Johnston et al. 1997), and there is evidence to suggest that female pygmy loris, *Nycticebus pygmaeus*, prefer to mate with such males (Fisher et al. 2003). That overmarking is involved in intrasexual competition in banded mongooses is further supported by the result that juveniles (prereproductive individuals) did not show sex-biased overmarking, but instead overmarked scents apparently indiscriminately. This result cannot be explained by a potential lack of sex specificity in juvenile scents, as only responses of juveniles to adult scents were recorded in the analyses and the proportion of encountered same-sex scents that were overmarked increased with age; the increase was most pronounced during the first 1.5 years of life, which coincides with sexual maturity.

Within females, the observed preference to overmark the scents of other females may also be explained by female intrasexual competition for males. Trivers (1972) suggested that the relative degree of competition for mates in the two sexes is determined by their relative expenditure on gametes and parental investment. As males typically invest less in both, competition is usually intense between males for access to females (Andersson 1994). However, in some species females may compete for males, particularly if males provide most of the parental care, as in callitrichid primates (see Goldizen 1986). Importantly, where male care exceeds female care in these small primates, rates of scent marking are strongly female biased (Heymann 2003), and it is possible that intrasexual overmarking in female banded mongooses may be related to the considerable pup care that males provide. After weaning, each pup forms a stable and almost exclusive attachment to a particular male (Gilchrist 2004), and this male 'escort' provisions its escorted pup almost exclusively (Gilchrist 2004). Perhaps an equally important factor to consider when discussing female competition for mates is the tightly synchronized oestrus observed within groups (Cant 2000). As multiple females are mate-guarded simultaneously (Cant 2000), one male cannot monopolize access to all females. Males may therefore benefit by choosing which female to focus their attention on, as older heavier females tended to be more likely to conceive and carried a larger number of fetuses (Hodge 2003). Although, in general, relatively little research has been conducted into scent marking in females (for exceptions see Johnston 1977; Hurst 1990; Coquelin 1992; Ferkin et al. 2004), evidence from other species suggests an association with intrasexual competition. For example, golden hamsters increase scent marking in response to female scent marks (Johnston 1977), and when they do mark in the vicinity of males this seems to stimulate male–male competition and could therefore increase their chances of mating with high-quality males (Fischer & Brown 1993).

Finally, further support for the hypothesis that overmarking is involved in intrasexual competition for mates and not for other resources is perhaps provided by the result that mongooses differed in their propensity to overmark scents of different types. Mongooses were more likely to overmark glandular secretions than excretory scent marks (urine and scats), and this result was similar for adults and juveniles. In general, glandular secretions tend to contain stable category-specific information in other species (e.g. European badger: sex: Buesching et al. 2002a, b, c; group: Davies et al. 1988; individual: Buesching et al. 2002a, c), and are less likely to convey information on, and vary with, reproductive physiology (e.g. ferret, no effect of oestrus: Clapperton et al. 1988). If overmarks are involved in intrasexual competition, we would expect selection to favour individuals that identify themselves (Tibbetts & Dale 2007), and so we might expect them to conduct 'scent wars' using scents that carry individual signatures, which mongoose urine, at least, does not appear to do

(N. Jordan, J. Hurst & R. Beynon, unpublished data). Excretory products are more likely to contain and convey information on reproductive state (e.g. giant panda, *Ailuropoda melanoleuca*: Swaisgood et al. 2002), and so may be more likely to be used for this than in competitive interactions. In addition, we found that same-group scents were overmarked in the same-sex-specific way regardless of whether they were encountered in regions of overlap with neighbouring groups or in areas of exclusive use. If scents were involved principally in territory defence we might expect them to be placed in isolation of each other, to increase the chance of detection by intruders. That overmarking is consistent throughout the home range fits with an intragroup function, as reproductive rivals within the resident group are present throughout, and not limited to areas of overlap with neighbouring groups.

In conclusion, mongooses have sex differences in scent composition and their responses to scents within their group support the idea that overmarking is involved in intrasexual competition. As resources other than mates, such as food, are not utilized in a sex-specific way, and since we found that consistent sex-specific overmarking develops around sexual maturity, this competition may be for mates or mating opportunities. In two companion papers, we focus on the specific patterns of overmarking within males and females separately, analyse individual signatures in scent marks, and assess the potential relationship between overmarking and reproductive success. In general, the role of scent overmarking is poorly understood, and focused behavioural studies on overmarking in a variety of species in the natural setting are required to expand on laboratory studies.

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APPENDIX

Coefficient estimates in all tables represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size.

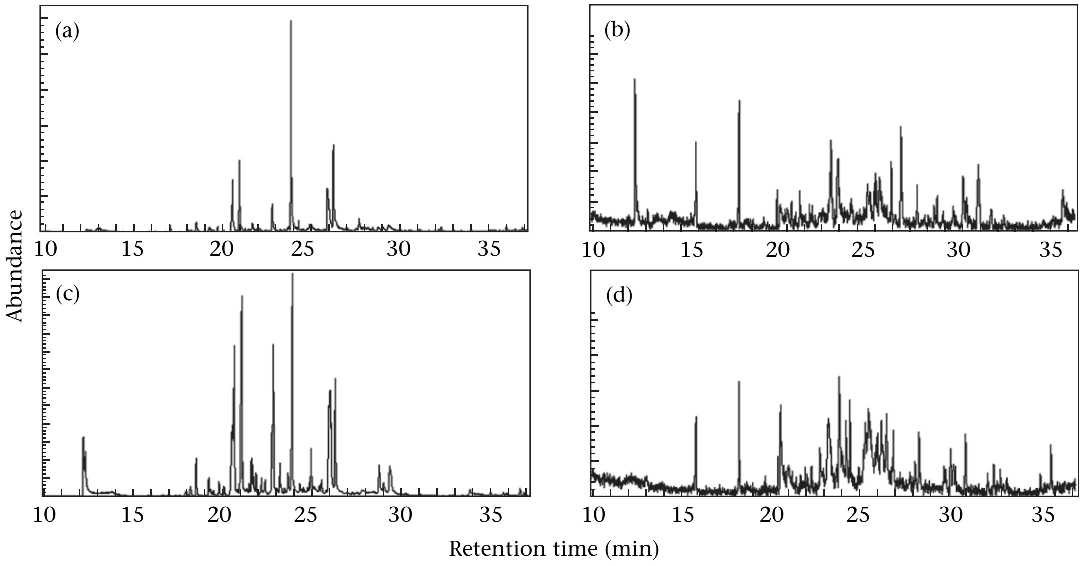

Figure A1. Gas chromatography profiles of anal gland secretions from (a, c) two adult male and (b, d) two adult female banded mongooses showing the typical sex differences in composition. Retention time (min) is shown against abundance (on an arbitrary scale).

Table A1

Generalized linear mixed model on the factors affecting the probability that individuals overmark an encountered single scent mark

		Wald statistic (χ^2)	*df*	*P*
Full model				
Investigator sex		0.49	1	0.485
Original marker sex		67.49	1	<0.001
Original mark type		30.55	4	<0.001
Original marker sex*Investigator sex		152.16	1	<0.001
Investigator sex*Original mark type		20.58	4	<0.001
Original marker sex*Original mark type		76.54	4	<0.001
Minimal model	Category	Coefficient estimate	SE	
Constant		2.662	0.5562	
Original marker sex	Female	0		
	Male	−2.329	0.5329	
Original mark type	Anal	0		
	Cheek	9.215		
	Token	−1.218	97.57 (0.3179−243.2)	
	Scat	−1.369		
	Urine	−1.383		
Original marker sex*Investigator sex	Male*Female	0		
	Male*Male	4.147	0.3362	
Investigator sex*Original mark type	Male*Anal	0		
	Male*Cheek	−9.176		
	Male*Token	−0.111	73.36 (0.3620−243.2)	
	Male*Scat	−1.109		
	Male*Urine	−0.968		
Original marker sex*Original mark type	Male*Anal	0		
	Male*Cheek	10.999		
	Male*Token	1.458	45.65 (0.3308−150.9)	
	Male*Scat	−1.059		
	Male*Urine	2.183		

Data were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0) indicating whether, following inspection of a scent mark, an individual overmarked the original mark. The analysis was conducted on data from 2038 encounters with single scent marks deposited by 158 adults and inspected by 159 adults from nine social groups. All five scent mark types (anal, cheek, token urine, urine, scat) were included. Group identity (estimated variance component = 0.00, SE = bound), Investigator ID (estimated variance component = 0.245, SE = 0.082), Original marker ID (estimated variance component = 0.088, SE = 0.068) and unique mark site (estimated variance component = 0.720, SE = 0.160) were included as random terms.

Table A2

Generalized linear mixed model on the factors affecting the probability that individuals overmark an encountered single token urination scent mark (the same terms were significant for all mark types)

		Wald statistic (χ^2)	*df*	*P*
Full model				
Investigator sex		1.57	1	0.210
Original marker sex		36.27	1	<0.001
Original marker sex*Investigator sex		161.21	1	<0.001
Minimal model	Category	Coefficient estimate	SE	
Constant		2.637	0.375	
Original marker sex	Female	0		
	Male	−3.334	0.5286	
Original marker sex*Investigator sex	Male*Female	0		
	Male*Male	7.795	0.6139	

The analysis was conducted on data from 823 encounters with single token urine scent marks deposited by 137 adults and inspected by 143 adults from eight social groups. Group identity (estimated variance component = 0.00, SE = bound), Investigator ID (estimated variance component = 0.173, SE = 0.162), Original marker ID (estimated variance component = 0.230, SE = 0.189) and unique mark site (estimated variance component = 0.506, SE = 0.280) were included as random terms.

Table A3

Generalized linear mixed model on the factors affecting the probability that individuals overmark an encountered double scent mark, where both previous marks are of the same type

		Wald statistic (χ^2)	*df*	*P*
Full model				
Investigator sex		3.08	1	0.079
Top marker sex		1.28	1	0.258
Original marker sex		0.62	1	0.432
Original mark type		17.7	4	0.001
Investigator sex*Top marker sex		19.34	1	<0.001
Minimal model	Category	Coefficient estimate	SE	
Constant		2.781	0.6129	
Original mark type	Anal	0		
	Cheek	−0.776		
	Token	−0.495	1.094 (0.5409−1.671)	
	Scat	−2.296		
	Urine	−1.848		
Original marker sex*Investigator sex	Male*Female	0		
	Male*Male	4.015	0.913	

The analysis was conducted on data from 298 encounters with double scent marks by 115 adult individuals from seven social groups. Double scent marks were made up of two scent marks of the same type deposited by different adult individuals, and this data set included original scents from 102 adults, and top scents from 105 individuals. All five scent mark types (anal, cheek, token urine, urine, scat) were included. Group identity (estimated variance component = 0.142, SE = 0.259), Investigator ID (estimated variance component = 0.00, SE = bound), Original marker ID (estimated variance component = 0.438, SE = 0.556), Top marker ID (estimated variance component = 0.00, SE = bound) and unique mark site (estimated variance component = 0.759, SE = 0.719) were included as random terms.

Table A4
Generalized linear mixed model on the factors affecting the probability that individuals overmark an encountered scent station (containing single or multiple scent marks of all types)

		Wald statistic (χ^2)	*df*	*P*
Adults				
Full model				
Investigator sex		0.00	1	0.947
Top marker sex		72.90	1	<0.001
Top mark type		85.21	4	<0.001
Top marker sex*Investigator sex		376.37	1	<0.001
Investigator sex*Top mark type		5.11	4	0.276
Top marker sex*Top mark type		82.72	4	<0.001
	Category	Coefficient estimate	SE	
Minimal model				
Constant		2.559	0.212	
Investigator sex*Top marker sex	Male*Female	0		
	Male*Male	3.747	0.1994	
Investigator sex*Top mark type	Male*Anal	0		
	Male*Cheek	0.5009		
	Male*Token	−0.6579	0.4018 (0.6845−0.2384)	
	Male*Scat	0.5060		
	Male*Urine	−1.1353		
Juveniles				
Full model				
Investigator sex		0.03	1	0.860
Top marker sex		0.05	1	0.825
Top mark type		22.07	2	<0.001
	Category	Coefficient estimate	SE	
Minimal model				
Constant				
Top mark type	Anal	0		
	Token	−1.899	0.608 (0.4747−0.7236)	
	Scat	−1.926		

The model for adult responses to scent marks includes only adult investigators of scents produced by adults (>365 days old; $N = 5952$ encounters with scent marks of five types [anal mark, token urine, urine, scat, cheek mark] at 1967 sites, involving 166 individual investigators [103 males, M, 63 females, F] and 167 donors [104M, 63F] from nine groups). Group identity (estimated variance component = 0.074, SE = 0.072), Investigator ID (estimated variance component = 0.132, SE = 0.042), Top marker ID (estimated variance component = 0.043, SE = 0.032) and unique mark site (estimated variance component = 1.138, SE = 0.122) were included as random terms. The model for juvenile responses to scent marks includes only juvenile investigators of scents produced by adults (<290 days; $N = 203$ encounters with scent marks of three types (anal mark, token urine, scat) at 150 sites, involving 74 individual investigators [43M, 31F] and 90 donors [60M, 30F] from six groups). Group identity (estimated variance component = 0.048, SE = 0.183), Investigator ID (estimated variance component = 0.043, SE = 0.307), Top marker ID (estimated variance component = 0.00, SE = bound) and unique mark site (estimated variance component = 0.823, SE = 0.555) were included as random terms.

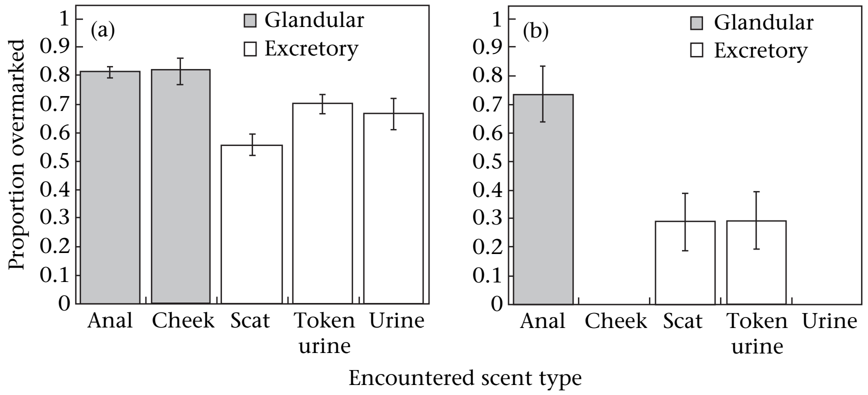

Figure A2. The effect of the encountered scent type (anal mark/cheek mark/scat/token urine/urine) on overmarking by (a) adults and (b) juveniles. Means ± SEs are shown and were generated from predicted means of the GLMM presented in Table A1. (Note that urine and cheek mark types were not included in the juvenile model as there were insufficient data.)

Table A5
Generalized linear mixed models on the factors affecting the probability that adult individuals overmark an encountered scent station

		Wald statistic (χ^2)	*df*	*P*
Token urination marks				
Full model				
Investigator sex		0.02	1	0.902
Top marker sex		49.99	1	<0.001
Top marker sex*Investigator sex		187.56	1	<0.001
	Category	Coefficient estimate	SE	
Minimal model				
Constant		2.437	0.290	
Investigator sex*Top marker sex	Male*Female	0		
	Male*Male	6.040	0.4410	
Urine marks				
Full model				
Investigator sex		12.32	1	<0.001
Top marker sex		48.68	1	<0.001
Top marker sex*Investigator sex		22.05	1	<0.001
	Category	Coefficient estimate	SE	
Minimal model				
Constant		1.256	0.361	
Investigator sex*Top marker sex	Male*Female	0		
	Male*Male	4.297	0.9150	
Scat marks				
Full model				
Investigator sex		0.01	1	0.925
Top marker sex		0.54	1	0.462
Top marker sex*Investigator sex		9.35	1	0.002
	Category	Coefficient estimate	SE	
Minimal model				
Constant		0.842	0.251	
Investigator sex*Top marker sex	Male*Female	0		
	Male*Male	1.2388	0.4050	
Anal marks				
Full model				
Investigator sex		6.07	1	0.014
Top marker sex		14.20	1	<0.001
Top marker sex*Investigator sex		168.88	1	<0.001
	Category	Coefficient estimate	SE	
Minimal model				
Constant		2.624	0.237	
Investigator sex*Top marker sex	Male*Female	0		
	Male*Male	3.6188	0.2785	
Cheek marks				
Full model				
Investigator sex		1.81	1	0.178
Top marker sex		1.92	1	0.166
Top marker sex*Investigator sex		2.71	1	0.100
		Coefficient estimate	SE	
Minimal model				
Constant		1.544	0.635	

Data were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0) indicating whether, following inspection of a scent station, an individual overmarked or not. Token urination marks model is based on 1279 encounters. Group identity ($N = 8$, estimated variance component = 0.00, SE = bound), Investigator ID ($N = 154$ [98 males, M, 56 females, F], estimated variance component = 0.111, SE = 0.133), Top marker ID ($N = 149$ [98M, 51F], estimated variance component = 0.292, SE = 0.169) and unique mark site ($N = 877$, estimated variance component = 0.960, SE = 0.283) were included as random terms. Urine marks model is based on 275 encounters. Group identity ($N = 8$, estimated variance component = 0.168, SE = 0.257), Investigator ID ($N = 103$ [68M, 35F], estimated variance component = 0.071, SE = 0.385), Top marker ID ($N = 87$ [54M, 33F], estimated variance component = 0.00, SE = bound) and unique mark site ($N = 168$, estimated variance component = 0.301, SE = 0.468) were included as random terms. Scat marks model is based on 763 encounters. Group identity ($N = 8$, estimated variance component = 0.063, SE = 0.089), Investigator ID ($N = 136$ [87M, 49F], estimated variance component = 0.279, SE = 0.136), Top marker ID ($N = 138$ [86M, 52F], estimated variance component = 0.00, SE = bound), and unique mark site ($N = 578$, estimated variance component = 0.780, SE = 0.232) were included as random terms. Anal marks model is based on 3458 encounters. Group identity ($N = 8$, estimated variance component = 0.103, SE = 0.103), Investigator ID ($N = 159$ [100M, 59F], estimated variance component = 0.057, SE = 0.054), Top marker ID ($N = 160$ [100M, 60F], estimated variance component = 0.041, SE = 0.057) and unique mark site ($N = 1162$, estimated variance component = 1.344, SE = 0.187) were included as random terms. Cheek marks model is based on 177 encounters. Group identity ($N = 6$, estimated variance component = 0.033, SE = 0.270), Investigator ID ($N = 83$ [61M, 22F], estimated variance component = 0.00, SE = bound), Top marker ID ($N = 82$ [55M, 27F], estimated variance component = 0.551, SE = 0.818) and unique mark site ($N = 98$, estimated variance component = 0.351, SE = 0.851) were included as random terms.

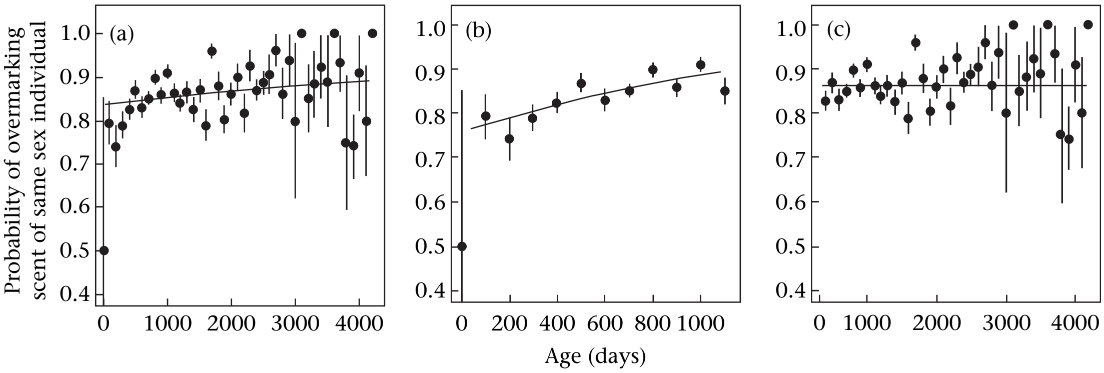

Figure A3. The relationship between the age of the investigator and the probability of it overmarking an encountered scent mark from the same sex. Points represent the mean ± SE for (a) all investigators (GLM: $F_{2,4730} = 2.14$, $P = 0.032$, mean ± SE effect of age = $1.139^{-5} \pm 5.323^{-5}$), (b) investigators from 0 to 3 years ($F_{2,2379} = 4.23$, $P < 0.0001$, mean ± SE effect of age = $0.911^{-3} \pm 0.215^{-3}$) and (c) adult individuals (>365 days; GLM: $F_{2,4496} = 0.641$, $P = 0.522$, mean ± SE effect of age = $3.618^{-5} \pm 5.645^{-5}$).