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Scent marking within and between groups of wild banded mongooses

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Abstract

Scent marking is commonly described as a territorial behaviour, and scent marks might deter potential intruders from entering occupied areas. Conspecific neighbours present both a reproductive and a territorial threat, thus, determining which, if any, of these threats shapes scent-marking behaviour is difficult. Banded mongooses *Mungos mungo* provide a rare clear separation between reproductive rivals (found within groups) and territorial rivals (neighbouring groups), because immigration into social groups is extremely rare, and mating occurs almost exclusively within groups. This situation offers an opportunity to assess the relative importance of territorial defence and intra-group competition for mates in shaping scent-marking behaviour. We combined detailed behavioural observations of scent marking, chemical analyses of scent composition and discrimination experiments in the field, and found little evidence for higher rates of scent marking in overlapping areas, a lack of group specificity of scents and a failure of individuals to discriminate between the scents of different groups. Although scent may fulfill some role in territorial demarcation and defence, these results suggest that scent marks and scent-marking patterns are also involved in communicating within social groups.

Introduction

Scent marking is widespread in mammals and is traditionally explained as a territorial behaviour designed to repel intruders (see Johnson, 1973 for review). More recent evidence, such as the failure of signals to repel territorial intruders (dwarf mongoose *Helogale parvula*, Rood, 1983; African lion *Panthera leo*, McComb, Packer & Pusey, 1994; meerkat *Suricata suricatta*, Doolan & Macdonald, 1996; North American beaver *Castor canadiensis*, Sun & Müller-Schwarze, 1998) and sex-specific responses to intruders (African lion, Pusey & Packer, 1997; spotted hyaena *Crocuta crocuta*, Boydston, Morelli & Holekamp, 2001), has led to the idea that scent may not function primarily in territory defence *per se*, but may instead be involved in direct competition for mates (Jordan, Cherry & Manser, 2007). However, an intruding individual or group commonly presents both territorial (i.e. food and space) and reproductive (i.e. mates and mating opportunities) threats to the resident(s). Thus, determining which of these threats is most important in shaping the scent-marking strategy is difficult.

Studies of scent marking commonly focus on species for which neighbouring groups or individuals are both territorial and reproductive rivals. In these species, scent-marking patterns consistent with both hypotheses (e.g. a border-marking 'strategy') are commonly interpreted as evidence for the more established theory of territory defence (see Gorman, 1984). Although a large body of evidence suggests that same-sex intruders are specifically targeted with actual physical aggression (spotted hyaena, Boydston *et al*., 2001), determining whether scent marks placed in the absence of intruders were deposited for territory defence, mate defence or both is difficult. In group-living banded mongooses *Mungos mungo*, territorial and reproductive rivals are two discrete entities. While neighbouring groups represent the main threat to territory loss or reduction (Müller & Manser, 2007), an individual's main reproductive rivals reside within the territory in the same social group. Banded mongoose scent marking therefore offers an opportunity to investigate and distinguish between the relative importance of scent marks for territory versus mate defence.

Banded mongooses are highly social small (<2 kg) carnivores living in large territorial family groups (8–70 individuals) (Cant, 2000; unpubl. data). Groups contain no clear dominant pair, and include a core of breeding adult males (2–15 males group^{-1}) and multiple (1–8) breeding females (Rood, 1975; Cant, 2000). Only 1/267 observed matings occurred with individuals from outside their own social group during the study period (unpubl. data; but see Cant, Otali & Mwanguhya, 2002 for an exception). Males compete

intensively with male relatives within their own social group for mating opportunities with close female relatives during highly synchronous oestrous periods (Cant, 2000). Immigration into existing stable social groups is rare (only two individuals joined an existing pack in 11 + years of observation; Bell, 2006). Despite this, mongooses are highly territorial and frequently interact aggressively with neighbours at the borders of their home range (Cant *et al.*, 2002; Müller & Manser, 2007). Home ranges overlap considerably (Gilchrist, 2001), and residents respond more strongly to simulated intrusions of neighbours than strangers (Müller & Manser, 2007). Neighbours represent a threat to residents not through reproductive competition, but through competition for food and space (large groups expanded their territories at the expense of smaller neighbouring groups; Müller and Manser, 2007). In addition, neighbours account for around 8% of adult mortalities, where the cause of death is known (unpubl. data). Like other carnivores (Macdonald, 1980), banded mongooses deposit a variety of eliminative (urine and faeces) and glandular scent marks (Müller & Manser, 2007): (1) anal marks are deposited by dragging the anal region across a horizontal object or surface; (2) cheek marks involve rubbing the side of the 'face' on horizontal or vertical objects and along the ground; (3) token (dance) urination is distinguished from (4) simple urination as it involves a stereotyped stamping of the hind legs; (5) faeces are deposited in token amounts at specific marking sites called latrines. Both sexes have well-developed scent glands in the anal region, and these feed into an exterior pouch, which is more developed and convoluted in males than in females. Although natural encounters with multiple foreign scents within the territory are probably extremely rare, previous presentation experiments using urine and faeces from other groups suggested that mongooses responded more strongly to the scents of same-sex individuals (Müller & Manser, 2008*a*). This supports the idea that scents may be important in intrasexual competition in this species.

To investigate whether scent marking was primarily involved in territory or mate defence, we focused on three key aspects of scents and scent-marking behaviour in wild banded mongooses. First, we conducted behavioural observations to determine the broad spatial patterns of scent distribution. Second, we collected scent samples to investigate the chemical/information content of scent secretions. Finally, we conducted experimental presentations in the field to determine whether mongooses could discriminate between the scent secretions of individuals from different social groups. If territory defence is the primary function of scent marking, then scents should be distributed to maximize the likelihood of intercepting territory intruders, perhaps through concentration of scents along territory borders. We might also predict a degree of group-specificity of scents, and that individuals would discriminate between the scents of different groups, in order to allow residents to identify themselves and intruders. In contrast, if the primary function of scent marking is mate defence, then scent marks should target reproductive rivals. In this case we might therefore expect scents to be distributed throughout the home range. A function in intrasexual competition within groups may not require group-specific scents and discrimination, but because these are negative predictions they are less robust than their alternatives.

Materials and methods

Study site and habituation

Data were collected from December 2005 to November 2007 on seven (in 2006) or eight (2007) 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: for details of the study area, see Cant, 2000). As part of a long-term study, five groups were habituated so that an observer was able to walk alongside a group as individuals foraged, and the majority of individuals could be followed to within 10 m without apparently interrupting their behaviour. The remaining three groups could be observed from a sitting position at distances of 5–50 m, and were visited a minimum of every 2–3 days. Group compositions and adult sex ratios are shown in Table 1.

Home-range estimation

Group location coordinates were collected on arrival at each group and at 15-min intervals during observation periods using handheld Garmin® (Garmin International Inc., Olathe, KS, USA) 12 global positioning system (GPS) units. To estimate group home ranges, we used the Animal Movement extension in ArcView® (version 3.3, Environmental Systems Research Institute, Redlands, CA, USA). We used the 95% fixed kernel method (Worton, 1989) with the least-squares cross-validation (LSCV) value for smoothing, as this provides the least-biased estimates of home range (Seaman *et al.*, 1999) and performs similarly to alternatives (Börger *et al.*, 2006). Home ranges were estimated separately for each study year to account for potential shifts in home ranges caused by the extinction of one group and the establishment of a new group in separate incidents in different parts of the study area. Home

Table 1 Adult group composition at the mid point of the study period (April 2007 for all groups, except group 'S' which were recorded in September 2007)

Group code	Total adults	M	F	Sex ratio (M/F)
B	25	17	5	3.40
D	11	6	5	1.20
F	22	15	7	2.14
G	9	4	5	0.80
H	22	18	4	4.50
S	8	5	3	1.67
T	25	18	7	2.57
V	11	7	4	1.75
Mean	16.625	11.25	5	2.25

M, male; F, female.

ranges were estimated from 764 ± 391 ($\pm$ SD) coordinates per pack (range: 204–1252) in 2006 and 607 ± 365 coordinates per pack (range: 139–1141) in 2007, which is sufficient for home-range analysis (Seaman *et al.*, 1999; Börger *et al.*, 2006). Areas of overlap with neighbouring groups were estimated, and groups were classified as 'neighbours' (some overlap of the 95% kernel) or 'strangers' (no overlap at the 95% kernel).

Spatial distribution of scent marks

Coordinates of all scent marks (anal mark, cheek mark, token urination, urination, faeces) where deposition was observed were recorded on a GPS. The densities of scent marks of each type in 'overlapping' regions (used by two or more groups) and 'exclusive' (non-overlapping) regions were calculated for each group (as the frequency of scent marks per km^2). Scent-mark densities and rates were used in paired comparisons within groups within years to control for potentially confounding differences in group size. To control for the possibility that scent-mark densities are artificially high in areas of greater utilization, scent-marking rates were calculated for each group and each scent-mark type in exclusive and overlapping areas, respectively, using the GIS kernels as estimates of time spent in each area. For example, if scent marking occurred at similar rates in exclusive and border regions, and mongooses spent 30% of their observation time in overlapping regions, then 30% of marks should be deposited in overlapping regions and 65% in exclusive regions (with 5% deposited outside the 95% utilization kernel). Scent-mark sites that contained clusters of mongoose faeces (>5 faeces within *c.* $2\,m^2$) were called 'latrines', and group encounters with these sites were recorded on occurrence. Latrine encounters were scored as such when the group passed through an existing latrine (i.e. one that contained mongoose faeces) and at least one individual investigated a faeces.

Trapping and identification

Individuals were trapped in box traps ($67 \times 23 \times 23$ cm; Tomahawk Live Trap Co., Tomahawk, WI, USA) for marking, collar application and collection of scent samples. Traps were tied open with wire and baited for several days with leftovers from local restaurants (mainly rice mixed with a few small pieces of cooked red meat and fish). Traps were set in the shade early in the morning and monitored at least every hour. Where specific individuals were targeted, an observer sat *c.* 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, carried to a nearby vehicle and driven to the laboratory (maximum distance <4 km). Following sampling and recovery from anaesthesia, individuals were released to their group, usually within 4 h. Trapping was conducted in accordance with ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching (Sherwin, 2006).

At the laboratory, individuals were coaxed from the traps into a black cloth bag tied around the entrance. Once inside the bag, the mongoose was held tightly against the closed end with an observer's foot. The captured individual's head was located and held firmly on either side with a gloved thumb and forefinger, and its nose was placed into a small 'gas mask'. This mask delivered an initial dose of 5% isoflurane from a specially calibrated vapourizer using oxygen as a vehicle at a flow rate of $2\,L\,min^{-1}$. Isoflurane is a halogenated volatile liquid, which maintains anaesthesia by depressing the central nervous system and has no known effect on fertility, pregnancy or offspring viability (Mazze, 1985). When fully anaesthetized (*c.* 2 min), the individual was removed from the bag, its nose was replaced into the mask and the dose was reduced and maintained at 3–3.5%. Following data collection and the renewal of an identifying haircut, isoflurane delivery was stopped, 100% oxygen was supplied for 5 s and the individual was placed back into the trap. Breathing rates of captured individuals were monitored throughout each procedure, and individuals regained normal locomotory ability after 1–7 min.

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. For rapid identification in the field, individuals were given a haircut in a unique position (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. Following tightening, excess plastic was cut off and the collar was prevented from tightening further by applying a drop of superglue into the ratchet mechanism. Collars and haircuts were renewed during routine trapping events. To enable groups to be located easily, one individual in each group was fitted with a refurbished Sirtrack® radiocollar (Sirtrack, Havelock North, New Zealand) weighing 22.85 ± 3.11 g ($\pm$ SD; range 17–28 g), which is 1.46% of the body mass (range 0.95–1.87%). Radiocollars were fitted following collaring procedures outlined for meerkats (Golabek, Jordan & Clutton-Brock, 2008) and were rotated among adult group members approximately every 6 months. If individuals developed sores as a result of the collars, these individuals were re-trapped and collars were immediately removed. Radiocollared animals were located using Telonics TR-4 receivers (Telonics Inc., Mesa, AZ, USA) from up to 1 km.

Scent sample collection

Anal gland secretion (AGS) and urine samples were collected under anaesthesia during routine trapping events, but additional monthly trapping sessions (December 2005–April 2006 inclusive) were conducted specifically for the collection of scent samples from target individuals. AGS was exuded directly from the gland into a 1.5 mL clean glass vial (Chromacol, Welwyn Garden City, UK) with a

PTFE-faced cap and septa (Chromacol) by applying gentle pressure immediately adjacent to the anal gland duct with the thumb and forefinger. Powder-free nitrile examination gloves were worn during this process and never contacted the anal gland opening or the collected secretion. Urine samples were collected during recovery from anaesthesia. To do so the anaesthetized individual was placed into a cleaned Tomahawk trap that had a cleaned stainless-steel tray (27×33 cm) fastened to its lower rear section. Traps were checked about every 10 min, and when a urine sample was produced the rubber straps were loosened and the tray was removed from below the trap. Samples were then poured down a pre-cut channel in one corner of the tray directly into a clean glass vial sealed with a PTFE-faced screw cap. Following collection of each sample, the vial was immediately resealed and transferred to a Nalgene® cryocane (Thermo Fischer Scientific Inc., Waltham, MA, USA) in an IC-35RX high-capacity liquid nitrogen refrigerator (International Cryogenics Inc., Indianapolis, IN, USA), where it was stored at –170 °C in liquid nitrogen. All samples were shipped to the Organic Chemistry Institute at the University of Zürich in Switzerland in a high-capacity IC-90VS dryshipper (International Cryogenics Inc.), and transferred to a −80 °C freezer immediately upon arrival and until analysis. All samples remained at −78.5 °C or below between collection and chemical analyses. Faeces were collected from known individuals at the time of deposition and held on ice until being presented to recipients 178.2 ± 19.4 ($\pm$ SE) min later (range: 48–667).

All glass vials and PTFE-faced Teflon screw caps used were soaked in absolute ethanol for 6 h before being thoroughly rinsed in natural spring water, which was collected from the Katwe municipal spring (0°11′40″S, 29°53′40″E). All water was filtered through a Brita® 3.0 L 'space saver' water purifier (Brita GmbH, Taunusstein, Germany) fitted with a Brita® classic filter cartridge, and cartridges were replaced after every 100 L. Ethanol is a polar solvent and cannot remove any mineral, oil, grease or animal fat contaminants. To remove these, vials were rinsed once with water then soaked for 1 h in non-perfumed Jireh® multipurpose liquid detergent (Sameg Chemical Products, Kampala, Uganda) diluted at an *c.* 1:100 ratio with filtered spring water, before being thoroughly and repeatedly rinsed with filtered spring water. Stainless-steel trays were scrubbed with a soft cloth in detergent and thoroughly rinsed in filtered water, and traps were similarly cleaned but with a hard brush. All vials, caps and stainless-steel trays were thoroughly sun-dried (for *c.* 90–120 min), and vials were tightly sealed with their caps until use.

Scent composition analyses

To determine whether scents were group-specific, chemical profiles for AGS samples were obtained by gas chromatography-mass spectrometry (GCMS) using a Hewlett-Packard 5890 Series II gas chromatograph (Urdorf, Zürich, Switzerland) fitted with an HP-5 column ($25\,\text{m} \times 0.2\,\text{mm}$ internal diameter; 0.33 μm film thickness in the stationary phase) and coupled to a Hewlett-Packard 5971 Series Mass Selective Detector. Analyses used one sample per individual, which were collected from three to nine (5.0 ± 1.93) females and two to 13 (7.88 ± 3.76) males per group from eight stable groups. Samples were removed from the −80 °C freezer in batches (containing randomly selected individual samples) on the day of analysis and held in the laboratory on dry ice (−78.5 °C). Vials were taken individually from dry ice and defrosted at room temperature. Defrosting occurred in *c.* 15 min. A few drops of 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 (for 30 s) before being filtered through medicinal cotton wrapped over the edge of a glass pipette. Powder-free nitrile gloves were worn throughout the sample preparation. Samples were run overnight using an HP 6890 series injector controlled by an HP GC autoSampler. One microlitre of the dissolved sample/solvent mixture was automatically injected directly into the column, which had a solvent delay of 2 min. The start temperature of 50 °C was increased by 8–240 °C min^{-1}, 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 remained 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). The mass detector operated in the electron impact ionization mode (70 eV), and data were collected in the total ion current mode (TIC). Relative TIC abundances are presented, and 35 discrete compounds were eluted between 10 and 37 min of the GCMS regime (Table 2). As we were primarily interested in broad differences in scent profiles across social groups, we did not attempt to validate compound identification with pure compounds, thus identification of the compounds listed are extremely tentative. Even using an identical analytical regime, the elution times for compounds differed slightly between chromatograms, and was therefore standardized. To standardize elution times between different chromatograms, we identified the compound that was found in the most samples ('C13' in Table 2). This compound was present in 62.1% of samples, and was eluted at 22 m42 s $\pm$ 1.485 s. All profiles were standardized to this value, with a range of 0 (where C13 was eluted at 22 m42 s or not detected) to 4.68 s added or subtracted to each elution time. We could not use the absolute abundance of peaks in our analyses as the quantity of eluted components may have differed between samples based on our method of sampling. Instead, individual peaks were matched by their retention times (accurate to 0.1 min), and the contribution of each peak to the overall area of the whole profile was calculated as a percentage of the total abundance of a sample (percentage abundance). If a certain peak could not be detected in a given profile, its percentage

Table 2 Retention times for chemical components of banded mongoose *Mungos mungo* anal gland secretion

Component	Retention time	Possible chemical component
c1	10.0–10.5	Phenol
c2	11.9–13.2	Benzene ethanamine
c3	15.8–16.0	1H-indole
c4	17.1–17.2	Not identified
c5	18.1–18.3	Not identified
c6	18.4–18.5	Decanedioic acid, didecyl ester
c7	19.1–19.3	2, 6-nonadienal, (E, E)-
		Dodecanoic acid
		Tridecanol
c8	19.6–19.9	Not identified
c9	20.0–20.1	Not identified
c10	20.4–20.8	1-tetradecanol
c11	20.9–21.1	Triacontane
c12	21.9–22.5	Propanoic acid, 2-methyl, 2-phenylethyl
		Butanoic acid
c13	22.7	Acetamide, *N*-(2-phenylethyl)
c14	22.8	Not identified
c15	23.1–23.5	3-eicosene, (E)
		9-eicosene, (E)
		1-tetracosanal
c16	23.7–24.0	Hexadecanoic acid
c17	24.2–24.5	Propanoic acid
		Butanoic acid, 3-methyl-, 2-phenylethyl
c18	24.6–24.9	1, 13-tetradecadiene
		1-hexadecanol
c19	25.0–25.2	Phosphonic acid, dioctadecylester
c20	25.3–25.6	Octadecadienoic acid
c21	25.7–25.9	9, 12,-octadecadienoic acid
c22	26.0–26.3	Not identified
c23	26.8–27.1	1-hexadecanol
		1-octadecanol
c24	27.2–28.2	9-octadecen-1-ol, (z)-
		Tetradecanol
c25	28.3–28.5	Tricosane
c26	28.6–28.9	Benzenepropanoic acid, methyl ester
c27	29.2–29.4	Not identified
c28	30.8–31.3	Acetamide, *N*-(2-phenylethyl)
c29	31.4–31.7	Acetamide, *N*-(2-phenylethyl)
c30	32.4–32.6	1-Octadecanol phosphonic acid, dioctadecylester
c31	33.8–34.1	Acetamide, *N*-(2-phenylethyl)
c32	35.8–36.0	Not identified
c33	36.1–36.3	Not identified
c34	36.4–36.6	Not identified
c35	36.7–37.0	Not identified

abundance was set as 0.001% and log-transformed (ln) for statistical analyses.

Group discrimination experiments

Field experiments using a modified habituation–dishabituation technique were undertaken to determine whether banded mongooses discriminate between scent stimuli from different groups. Experiments followed the methodology of Johnston (1993). In these experiments, an individual foraging naturally was approached and presented with a stimulus three times (sufficient for its response to wane in preliminary trials), at which point a second stimulus was introduced. If the individual can discriminate between the two stimuli, an elevated response is expected to the 'novel' stimulus. Stimuli used in each experiment were constant and either (1) AGS; (2) faeces; or (3) urine. To ensure that samples were of the same effective age as each other at the time of presentation, their removal from liquid nitrogen was staggered by 10 min, in line with the intended inter-presentation time in the field. Samples were transported to the field on ice, and immediately before AGS presentations, a small droplet (about 0.05 mL) of secretion was removed from its vial on the end of stainless-steel forceps and dropped onto a clean glass slide that had been wrapped in a 12×8 mesh absorbent cotton gauze roll. For urine experiments, 0.5 mL was presented in the same fashion. Faeces were removed from ice 10 min before they were presented to the target mongoose on a small clean plastic tray. To control for differing familiarity, all experiments compared the response of individuals to samples from two 'neighbour' groups or two 'stranger' groups. In all cases, the recipient was presented with four samples at 10-min intervals, and all samples within an experiment were collected from adults (>1 year) of the same sex as each other. Where possible, the target individual was the same sex as the scent donors, but this was not always possible because of group size, group composition and individual habituation constraints. In presentations of scents from neighbours, recipients were of the same sex as the donors in 16/24 experiments, and in 15/25 stranger scent experiments. The first three samples (A1, A2, A3) were from three different individuals from the same group as one another, and the final sample (B) was from an individual from a second group. Investigation durations of the recipient (time spent licking the sample or with its nose within 1 cm) were recorded on a tripod-mounted camcorder (JVC miniDV digital video camera, model GR-D240EK, JVC Americas Corp., Wayne, NJ, USA), and measured to the closest frame (30 frames s^{-1}) using Panasonic MotionDV Studio after semi-blind extraction (measurements were conducted by N. R. J. on randomly labelled clips 18 months later). After the recipient moved 20 cm or more from the sample, 5 min of focal data on vigilance were recorded using a hand-held Psion II data logger (model LZ-64, Psion Teklogix, Mississanga, ON, Canada). Individuals were considered vigilant when they were bipedal or quadrupedal and immobile with the head raised above ground and not engaged in any other activity, and individual bouts were separated by a change in activity. The distance travelled post-presentation was quantified using GPS.

Statistical analyses

All statistical tests were parametric and carried out with SPSS 15.0 (SPSS Inc., Chicago, IL, USA). We checked the

normality of data using the Kolmogorov–Smirnov test and log-transformed (ln) non-normal data. Planned *post hoc* least-significant difference (LSD) tests were only conducted on significant ANOVA [to test experiment data for habituation (A1 vs. A3) and discrimination (A3 vs. B)]. All results are presented as mean ± SE unless stated otherwise. To reduce the dimensionality of the chemical data, a principal components analysis (PCA) was performed using the Kaiser method (Kaiser, 1960). These principal components were then entered into a discriminant function analysis (DFA). DFA identifies linear combinations of these principal components and assigns each sample to its appropriate group (correct assignment) or to another group (incorrect assignment) using this information. For external validation we used a leave-one-out cross-validation procedure and estimated the significance levels for correct statistical assignment of scents to their source category (i.e. the group, sex or individual from which they were collected) using *post hoc* 'bootstrapping' analyses that were conducted in 'R' (R Development Core Team, 2008). This method determined the probability that a cross-validated correct assignment value was achieved by chance, and followed the methods of Müller & Manser (2008*b*).

As analyses involved the percentage contribution to the overall profile of each compound, these compounds are referred to as c1–c35, respectively. To control for the potential that scents were sex-specific, scents from males and females were treated separately in analyses.

Results

Mongooses encountered more scent marks in regions of their home range that overlapped with those of other groups than in areas of exclusive use, but this was probably not because of elevated rates of deposition in these regions. Groups also did not have group-specific scents, and individuals did not discriminate between scents from different groups.

Spatial distribution of scent marks

The mean home-range areas were similar for the same group in different years (paired *t*-test: $t = -0.807$, d.f. = 6, $P = 0.450$). 2007 ranges overlapped 2006 ranges by 85 ± 2.5% (range 76.8–93.4). Yearly home-range areas, percentage overlaps and perimeter lengths are presented in Table 3.

In both years, groups encountered latrines at higher densities in overlapping versus exclusive areas of their home ranges [paired *t*-test: (2006) $t = 3.309$, $n = 6$, $P = 0.021$; (2007) $t = 2.039$, $n = 8$, $P = 0.081$) but not significantly so in 2007. In 2006, groups encountered 156.9 ± 35.3 (range 65.6–321.5) latrines km^{-2} in overlapping regions, compared with 109.3 ± 29.1 (6.83–216.2) in exclusive areas. In 2007, groups encountered 99.9 ± 30.3 (11.2–231.4) latrines km^{-2} in overlapping regions and 58.7 ± 17.5 (10.3–158.1) in exclusive areas. However, this increased encounter rate with scents could be attributed to the increased number of individuals (i.e. from at least two groups) that used overlapping regions compared with the number that used exclusive regions. If individuals scent marked at similar rates regardless of their location in their home range, individuals would be expected to encounter more scents in overlapping regions. To test this, we looked at marking rates in the two regions. In 2006, scent marks tended to be deposited at higher rates in overlapping regions (paired *t*-test: $t = 2.094$, $n = 7$, $P = 0.081$; Table 4), with 13.6 ± 4.58 scent marks deposited per estimated unit time in overlapping regions and 7.5 ± 2.05 in exclusive regions. However, this trend disappeared in 2007, with scent marks deposited at similar rates in both regions ($t = 0.138$, $n = 7$, $P = 0.895$; 19.9 ± 13.7 in overlapping regions, 17.1 ± 10.6 in exclusive regions; Table 4).

Table 3 Home-range areas, perimeter lengths and percentage home range overlaps for study groups

Measure	Year	Mean	SE	Range	*n*
Home-range area (km^2)	2006	0.82	0.15	0.40–1.46	7
	2007	0.88	0.11	0.30–1.32	8
Home-range perimeter (km)	2006	4.94	0.50	3.70–7.49	7
	2007	5.40	0.31	4.59–6.84	8
Percentage overlap	2006	40.28	8.57	24.56–81.53	7[a]
	2007	45.20	9.40	16.11–68.84	8[b]

[a]Range data are based on $n=6$, excluding group V (11%) which neighboured groups with unknown ranges.
[b]Range data are based on is $n=6$, excluding group V (4.7%) which neighboured groups with unknown ranges and group S (92.5%) which was in the process of establishing its range.

Chemical composition of scent marks

Males

Seven principal components, explaining 81.0% of the variance, were derived from log-transformed percentage abundances of each of 35 eluted compounds from the AGS of 63 adult males from eight stable social groups. A DFA based on these principal components correctly classified 38.1% of (cross-validated) samples to their social group (compared with 14.99% expected by chance; Fig. 1a). To allow a *post hoc* bootstrapping analysis, this dataset was restricted to a subset of 42 individuals (seven adult males in each of six stable social groups). The first seven principal components derived from their AGS explained 81.2% of the variance in the data. 26.2% were correctly assigned to the correct social group, which is not significantly higher than the 16.67% correct assignment expected by chance (bootstrapping; $P = 0.115$).

Females

Eleven principal components, explaining 81.2% of the variance, were derived from log-transformed percentage abundances of each of 35 eluted compounds from the AGS of 40 adult females from eight stable social groups. A DFA

Table 4 Deposition rates for each scent-mark type in different regions of the home range in 2006 and 2007

	2006						2007					
Scent-mark type	*t*	d.f.	*P*	HR region	Mean	SE	*t*	d.f.	*P*	Region	Mean	SE
Investigation	2.144	5	0.085	Overlapping	11.34	3.42	0.156	6	0.881	Overlapping	15.00	10.40
				Exclusive	5.93	1.24				Exclusive	13.34	8.45
Dance	2.478	5	0.056	Overlapping	1.98	0.60	0.21	6	0.841	Overlapping	3.66	2.32
				Exclusive	1.20	0.34				Exclusive	3.24	2.41
Faeces	1.972	5	0.106	Overlapping	5.66	1.85	0.147	6	0.888	Overlapping	5.41	3.70
				Exclusive	3.04	0.94				Exclusive	5.13	3.12
Anal	2.089	5	0.091	Overlapping	7.55	2.22	0.134	6	0.898	Overlapping	10.14	7.21
				Exclusive	4.04	0.87				Exclusive	8.13	4.81
Cheek	1.704	5	0.149	Overlapping	0.66	0.22	−0.562	6	0.595	Overlapping	0.16	0.10
				Exclusive	0.31	0.08				Exclusive	0.29	0.16

Investigation rates are also shown, and paired *t*-tests compare rates in overlapping and exclusive areas of the home range.

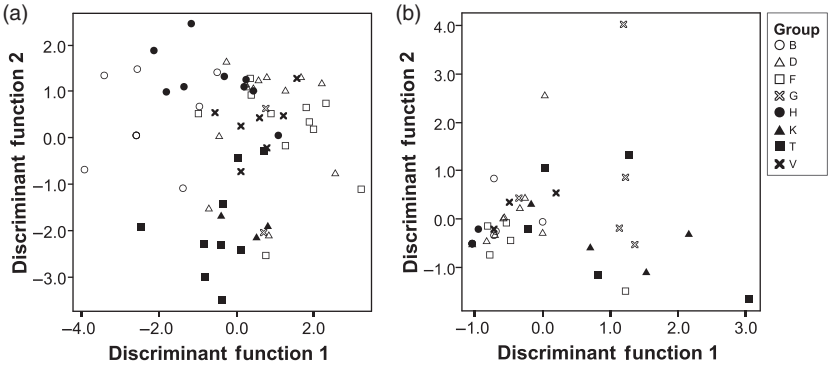

Figure 1 Comparison of chemical profiles of anal gland secretion collected from 63 male adult banded mongooses *Mungos mungo* (a) and 40 female adults (b). Each individual contributed only one scent sample to the data set (December 2005–April 06). Discriminant functions 1 and 2 were generated from seven principal components (from a correlation matrix) derived from log-transformed percentage abundances (percentage of total compounds eluted from 10 to 37 min) of 35 distinct compounds eluted during gas chromatography-mass spectrometry analyses.

based on these principal components correctly classified 35% of (cross-validated) samples to their social group (compared with 14.13% expected by chance; Fig. 1b). To allow a *post hoc* bootstrapping analysis, this data set was restricted to a subset of 24 individuals (four females in each of six stable social groups). The first 10 principal components derived from their AGS explained 85.9% of the variance in the data. 33.3% were correctly assigned to the correct social group, which is not significantly higher than the 20.0% correct assignment expected by chance (bootstrapping; $P = 0.126$).

Group discrimination experiments

Mongooses did not discriminate between individuals from groups of equal familiarity on the basis of AGS, urine or faeces. Although mongooses did habituate to sequentially presented scents from individuals of one group, *post hoc* tests revealed that they did not show elevated investigation to the scent of an individual from a different group (Table 5; Fig. 2). *Post hoc* (LSD) tests on a significant repeated measures ANOVA ($F_{3,27} = 3.549$, $P = 0.028$) confirmed that although mongooses did habituate to sequential presentations of urine from three different individuals of a single neighbouring group (A1 vs. A3, $P = 0.025$), they did not discriminate between urine from individuals from two different neighbouring groups (A3 vs. B $P = 0.296$). Similar patterns were evident for stranger urine ($F_{3,27} = 5.299$, $P = 0.005$, A1 vs. A3, $P = 0.009$; A3 vs. B, $P = 0.456$), and stranger AGS ($F_{3,21} = 3.275$, $P = 0.041$; A1 vs. A3, $P = 0.006$; A3 vs. B, $P = 0.258$). All other repeated measures ANOVA were not significant (Table 5). Additionally, vigilance rate (measured as the number of bouts an individual raised its 'nose' above vertical each minute), mean vigilance bout length and the percentage of observation time spent vigilant were not affected by the presentation of samples of any type (Table 5). Instead, individuals maintained baseline levels of vigilance following exposure to all foreign scents (Fig. 3). Mongooses also did not significantly alter the distance they moved in the 10 min following presentation of foreign samples (Fig. 4).

Discussion

Scent marking in mammals is traditionally interpreted as a territorial behaviour (Johnson, 1973), but intruders usually present both a reproductive and a territorial threat. Therefore, determining whether the threat of food/space loss (territory defence) or the threat of loss of mates or mating opportunities is more important in shaping scent-marking patterns has proven particularly difficult to determine. In banded mongooses, where individuals are either

Table 5 Results from repeated measures ANOVA on the response of recipients to habituation–dishabituation experiments with scent

		Scent type								
		Urine			Faeces			AGS		
Treatment	Response	*F*	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Neighbours	Investigation duration	3.55	3,27	0.028*	2.06	3,24	0.132	2.69	3,24	0.069
	Vigilance rate (bouts min^{-1})	0.42	3,27	0.737	1.33	3,24	0.288	0.26	3,24	0.851
	% time vigilant	0.02	3,27	0.995	1.23	3,24	0.321	0.99	3,24	0.414
	Mean vigilance bout length	0.17	3,27	0.918	0.52	3,24	0.675	0.86	3,24	0.474
	Distance travelled	1.04	3,18	0.400		(*n*=5)		2.19	3,21	0.120
Strangers	Investigation duration	5.30	3,27	0.005*	1.81	3,21	0.177	3.28	3,21	0.041*
	Vigilance rate (bouts min^{-1})	1.44	3,27	0.252	0.18	3,21	0.908	0.14	3,21	0.137
	% time vigilant	0.89	3,27	0.461	0.39	3,21	0.762	1.05	3,21	0.393
	Mean vigilance bout length	1.32	3,27	0.288	1.31	3,21	0.298	0.67	3,21	0.580
	Distance travelled	1.04	3,24	0.392	1.06	3,18	0.392	0.30	3,18	0.825

Subjects were presented with either urine, faeces or anal gland secretions from two neighbouring groups (three sequentially from the first group, followed by one from the second group) or two stranger groups. The recipients investigation duration of the scent, and subsequent measures of vigilance and distance travelled were compared.
*Significance at the 0.05 level.
AGS, anal gland secretion.

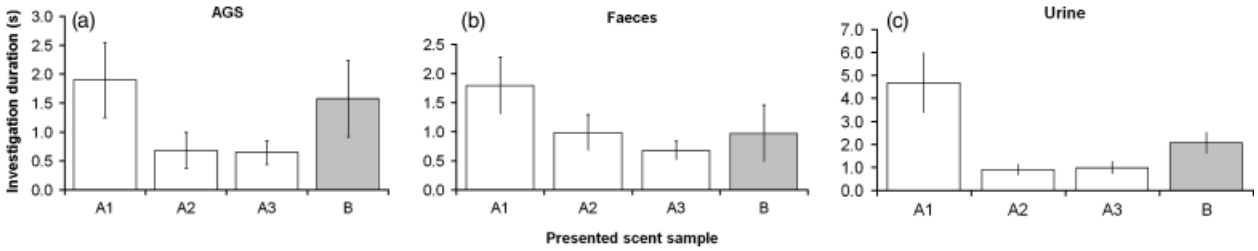

Figure 2 Mean (± SE) number of seconds individuals spent investigating three different scent-source types (a, AGS *n*=8; b, faeces *n*=8; c, urine *n*=10) from three different individuals of a 'stranger' group during habituation trials (A1–A3), and an individual of a different 'stranger' group during test trial B.

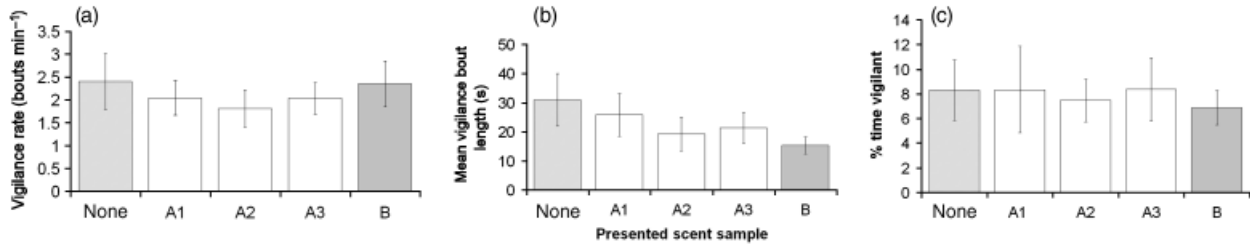

Figure 3 Mean (± SE) for three measures of vigilance (a, vigilance bouts per minute *n*=8; b, vigilance bout length *n*=10; c, percentage time spent vigilant *n*=8) during experimental presentation of urine from three different individuals of a stranger group. 'None' refers to the 10-min period before exposure to the first sample.

reproductive rivals or territorial rivals only, evidence suggests that scent marks and scent-marking patterns are involved in communicating with individuals within social groups, in addition to an inter-group function. Our results show that scents are placed throughout the home range, but are more frequently encountered in regions that overlap with the home ranges of other groups. However, as groups generally scent marked at similar rates in overlapping and exclusive regions, the increased density of scent marks in overlapping regions may be explained by multiple groups using these regions. Additionally, we found neither evidence of group specificity in mongoose AGS, nor any evidence to suggest that individuals discriminate between different groups of equal familiarity on the basis of scents. Taken

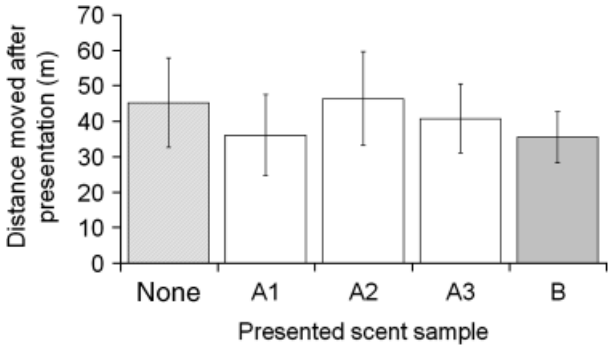

Figure 4 Mean (± SE) distance travelled in 10 min following presentation of anal gland secretion samples from three different individuals of a stranger group during habituation trials (A1–A3), and an individual of a different non-neighbouring group during test trial B. The hatched bar shows the distance moved before presentation of sample A1 (i.e. the baseline). 'None' refers to the 10-min period before exposure to the first sample.

together, these results suggest that scent marking may be important in intra-group communication, in addition to their potential role in territory defence.

As scent marking may involve significant investments in time and energy, individuals may increase the efficiency of signal transfer by depositing scent marks in specific locations, which maximize the chance that the intended recipient(s) will discover the scent(s) (Gorman & Trowbridge, 1989; Gosling & Roberts, 2001). Many species preferentially scent mark along or close to territory borders (European badger *Meles meles*, Kruuk, 1978; golden jackal *Canis aureus*, Macdonald, 1979; spotted hyaena, Gorman & Mills, 1984; grey wolf *Canis lupus*, Peters & Mech, 1975; aardwolf *Proteles cristatus*, Richardson, 1990; Eurasian beaver, Rosell & Thomsen, 2006), perhaps to maximize interception by territorial intruders. As in banded mongooses, encounters with territorial neighbours consistently occur in border regions of the range (pers. obs.); a clear pattern of border marking would emerge if residents specifically targeted neighbouring groups with their scents. Instead, scents were placed throughout the home range, suggesting that scents may also be involved in intra-group communication. Although banded mongooses tended to scent mark at higher rates in overlapping border regions in 1 year, this tendency was not significant for any scent-mark type, but scent marks were encountered at higher densities in overlapping regions. This may result from the greater number of individuals (multiple groups) using these areas. This is an often overlooked and potentially confounding factor in studies using survey methods alone to determine the spatial distribution of scent marks in the environment, and may further exaggerate the suggested preference for border marking.

Too much emphasis on the spatial distribution of scents may be misleading (Gosling & Roberts, 2001). First, as Macdonald (1980) realized for faeces, only group-living species may be able to produce enough scent to maintain border latrines. Although many mammals scent mark along territory borders (Macdonald, 1985), scent marks may be distributed throughout a territory where regularly patrolling and maintaining a set of border latrines is not feasible (e.g. Gorman & Mills, 1984; Gorman, 1990). Such a strategy is not inconsistent with a territorial function (Gosling & Roberts, 2001), as scent-matching would allow intruders to unambiguously identify the owner regardless of the spatial distribution of scents (e.g. Gosling, 1982; Gosling & McKay, 1990). Scents should therefore be placed in locations likely to maximize the chance of intercepting intruders, if intruders are the target recipients.

In other species that scent mark throughout their range (e.g. Iberian wolf *C. lupus*, Barja, de Miguel & Barcena, 2005; African civet *Civettictis civetta* and spotted hyaena, Bearder & Randall, 1978; yellow mongoose *Cynictis penicillata*, le Roux, Cherry & Manser, 2008), non-border marking 'patterns' are also, rather counter-intuitively, interpreted as territorial marking (Bowen & McTaggart Cowan, 1980). Scent marking throughout a range may represent the most efficient scent-marking strategy when the costs of patrolling/peppering the border are high (e.g. Gorman & Mills, 1984; Gorman, 1990). Non-border marking is usually associated with paths, trails and junctions (e.g. Barja, de Miguel & Barcena, 2004) and so may be economical when intruders use predictable paths (Gorman, 1984). In contrast the non-border, scent-marking pattern in banded mongooses is probably uncommon. Intrusions deep into mongoose territories are rare by neighbouring groups and almost unknown for loners (pers. obs.); thus, such a marking 'strategy' seems unlikely to be directed at potential intruders. Instead, this pattern is probably directed towards individuals within their own group.

In contrast to many other species (European badger, Gorman, Kruuk & Leitch, 1984; Buesching, Waterhouse & Macdonald, 2002; Bechstein's bat *Myotis bechsteinii*, Safi & Kerth, 2003), different social groups did not have statistically distinct scent profiles. In addition, we found little evidence to suggest that mongooses discriminate between the scents of different groups. Whereas previous studies have generally failed to control for a potential familiarity effect in experiments of group discrimination, either comparing 'own group' with 'other group' (big brown bat *Eptesicus fuscus*, Bloss *et al.*, 2002, Columbian ground squirrel, Hare, 1994) or neighbours with strangers (e.g. European badger, Palphramand & White, 2007), we controlled for this by comparing mongooses' ability to discriminate between scents from two neighbouring groups or from two stranger groups. Using investigation duration as the response term, we found that although recipients habituated to the sequential presentation of scents from one group, they did not dishabituate when presented with a scent from a different group, suggesting that they did not discriminate between groups on the basis of scent. These results were consistent in experiments with AGS, urine, and faeces and for both neighbour and stranger presentations. Furthermore, experimental exposure to scent stimuli did not affect vigilance or the distance moved by recipients immediately post-presentation. This lack of discrimination is surprising. Perhaps recipients *recognize* (an unobservable neural

process) scent differences, but do not *discriminate* (a measurable behavioural response), because a single intruding individual may not pose a threat to an individual living in a group. This interpretation is supported by the finding of Müller & Manser (2007) that groups presented with multiple samples from neighbours on the incorrect border responded more strongly than to neighbours on the correct border. Their work suggests that individuals know where to expect particular neighbours and that either multiple scent sources are necessary for inter-group recognition or required to simulate a substantial enough threat to warrant a large and measurable response. In this study, group discrimination experiments based on sequential single sample presentations may not be sufficient to test group discrimination, or residents do not need to determine to which group an intruder belongs. However, the latter is probably not the case as individuals did sometimes respond to single scents by recruiting others.

In summary, this multidisciplinary investigation into the function of scent marks in banded mongooses suggests that scents may not be exclusively involved in territory defence, but may also serve an important intra-group function. As previous work on the function of scent marking has focused on species where neighbours represent dual threats of reproductive and territory loss, the importance of scent marking in territory defence *per se* may have been over emphasized, and other functions such as reproductive competition may be an important driving force behind this widespread behaviour. This study highlights the need to investigate communication in species where the impact of reproductive and territorial rivals can be teased apart.

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