

Original Article

Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation

Rafael Mares,^a Andrew J. Young,^b Danielle L. Levesque,^a Nicola Harrison,^a and Tim H. Clutton-Brock^a

^aDepartment of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK and

^bCentre for Ecology and Conservation, University of Exeter, Cornwall Campus, Tremough, Penryn, Cornwall TR10 9EZ, UK

Although sex-specific responses to intruder scent marks have been described in many mammal species, less is known about variation in responses in cooperatively breeding species where differential access to breeding opportunities exists within groups. When reproductive skew is high, strong responses to extragroup breeding rivals would be expected mainly from dominant individuals, with levels of investment depending on female receptiveness. However, evidence from controlled experiments on cooperative breeders for sex and social status differences in responses to intruder scent marks is limited. Here, we investigated responses to intruder scent marks in cooperatively breeding meerkats (*Suricata suricatta*), where a single dominant pair largely monopolizes within-group reproduction. A series of experimental presentations using feces were used to test first, whether meerkats discriminate between resident and extragroup male scent marks; second, whether sex and social status affect the response to intruding male scents; and third, whether dominant males increase their level of response when dominant females are most receptive. Our results suggest that meerkats are able to discriminate between resident and intruding male scent marks and show that dominant males have the strongest overall response to intruder scent marks, which does not increase with female receptiveness. We suggest that, although all group members may be affected by the presence of intruders, reproductive conflict may be the main reason for the stronger response of dominant males to extragroup male scent marks in this cooperatively breeding species with high reproductive skew. **Key words:** extragroup mating, mate defense, mate guarding, presentation experiment, prospecting, reproductive conflict, scent marking, *Suricata suricatta*. [*Behav Ecol* 22:594–600 (2011)]

INTRODUCTION

Scent marking plays a fundamental role in communication in many mammal species, allowing information, such as the species, sex, individual identity, health, and reproductive status of a signaler to persist in the environment (Wyatt 2003; Johansson and Jones 2007). This information may advertise competitive abilities (Hurst and Beynon 2004), thus, scent marking with urine, feces, and scent gland secretions has traditionally been associated with territoriality and resource defense (Gosling and Roberts 2001). Resource holders tend to scent mark more than others and, in territorial species, they respond to scent marks of intruding individuals in ways that reflect the level of threat posed by the intruder (Johnson 1973; Gosling and Roberts 2001; Hurst and Beynon 2004). Strong intrasexual competition over resources, such as food, shelter, and mates (Boydston et al. 2001; Cant et al. 2002), therefore predicts that individuals will respond most aggressively toward scent marks of intruders of the same sex (Gosling and Roberts 2001; Palagi and Dapporto 2007). In gregarious species, cooperative resource defense among same-sex individuals is fairly common (e.g., lion, *Panthera leo*;

Heinsohn et al. 1996; common marmoset, *Callithrix jacchus*; Lazaro-Perea 2001; and chimpanzee, *Pan troglodytes*; Wilson et al. 2001), yet differences in social status may also affect responses to intruders (e.g., naked mole-rat, *Heterocephalus glaber*; O’Riain and Jarvis 1997; Damaraland mole-rat, *Cryptomys damarensis*; Cooney 2002) and to their scent marks (reviewed in Thiessen and Rice 1976; e.g., house mouse, *Mus domesticus*; Hurst 1990).

In cooperatively breeding species, social status often determines access to breeding opportunities, and the distribution of reproduction within groups may affect whether breeding rivals come from within or outside the group. In the banded mongoose (*Mungos mungo*), a species with relatively low reproductive skew, males reflect competition for mates within their groups by selectively countermarking male scent marks from their own group (Müller and Manser 2008). In contrast, when reproductive skew is high and breeding rivals are likely to come from outside the group, strong responses would be expected toward intruder scent marks, primarily from dominant individuals who have more to lose in terms of breeding opportunities. In addition, dominant males may vary their response depending on female receptiveness (Müller and Manser 2008). Constraints on subordinate dispersal and breeding along with the indirect fitness benefits accrued through the reproduction of closely related breeders (Emlen 1991) may also lead to strong responses to intruders from subordinate individuals. To our knowledge, there are no controlled experiments investigating sex and social status differences in responses to intruder scent marks in cooperative breeders with high reproductive skew.

Address correspondence to R. Mares. E-mail: crm53@cam.ac.uk.
D.L. Levesque is now at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa.

Received 7 October 2010; revised 7 February 2011; accepted 9 February 2011.

In this study, we investigated individual responses to intruder scent marks in meerkats (*Suricata suricatta*), a cooperatively breeding species of mongoose that live in groups of up to 50 individuals, where a single dominant pair largely monopolizes within-group reproduction (Griffin et al. 2003; Spong et al. 2008). Dominant individuals are typically unrelated to each other, and inbreeding with offspring and siblings that remain in the group as subordinate helpers is avoided (Spong et al. 2008). Ultimately, subordinates of both sexes may disperse from the natal group, but unlike females, males leave voluntarily and conduct extraterritorial prospecting forays prior to dispersal (Young et al. 2007). During these forays, prospectors regularly approach foreign groups and may mate with both dominant and subordinate females, leading to appreciable levels of extragroup paternity (Young et al. 2007; Spong et al. 2008). Prospecting male coalitions can also take over established breeding groups, ejecting all adult resident males in the process (Doolan and Macdonald 1996; Young 2003). Previous studies suggest that resident males respond most aggressively to intrusions by prospecting males (Doolan and Macdonald 1996; Young et al. 2005), yet a detailed analysis of the effects of sex and social status on the individual behavioral responses to prospectors has not been done.

Here, we investigated the responses of meerkats of different sex and social status to scent marks of prospecting males, as territorial intruders. Prospecting males regularly deposit feces and anal marks (Jordan 2007) in conspicuous locations on encountering foreign groups (Mares R, Levesque D, Harrison N, personal observation), presumably as a form of advertisement to potential mates. Previous studies on scent-marking behavior in meerkats have focused on latrines, where both dominant and subordinate males scent mark significantly more than females and overmark female scent marks more frequently than those of other males from their own group (Jordan 2007). However, besides anecdotal evidence (Doolan and Macdonald 1996; Manser 2001), it is unclear whether meerkats respond differently to extragroup scent marks than to those from their own group members. We therefore conducted a series of fecal presentation experiments on groups of wild meerkats to determine, first, whether meerkats respond differently to resident and extragroup subordinate male scent marks, and second, whether responses to extragroup scents differ between resident individuals of different sex or social status. We also investigated whether dominant males change their response to these foreign scent marks depending on the reproductive status of the resident dominant female. We predicted that all meerkats would have a distinct response to extragroup scent marks compared with resident scents and that there would be differential responses among individuals to extragroup scents according to threat. Given the greater risk of reproductive competition between intruding males and resident dominant males, compared with dominant females or subordinate individuals, we expected that dominant males would show the strongest response to intruding male scent marks. We also predicted that dominant males would further increase their level of response when resident dominant females were in estrus.

METHODS

Study area and population

The study was conducted on a wild population of meerkats at the Kuruman River Reserve (lat 26°59'S, long 21°50'E) and surrounding ranch land in the southern Kalahari desert, South Africa, during the 2008 and 2009 breeding seasons (September–February). Details on climate and habitat at the study site and female fertility patterns of the study population are described elsewhere (Russell et al. 2002; Young et al.

2007). The meerkats in the population are habituated to close observation (within 2 m), are individually identifiable by unique dye-marks on their fur and have known life histories, as groups are visited at least once every 3 days. Individuals are accurately categorized by social status as either dominant or subordinate, as subordinate individuals are behaviorally submissive to the dominant individual of the same sex in their group (Carlson et al. 2004).

Fecal sample collection and presentation

Feces from subordinate males were collected ad libitum immediately after deposition. Two-thirds of each deposit were placed in individual plastic bags and put into a flask with ice, leaving the rest of the sample at its original location to avoid disrupting its potential communicative value. Samples were transferred to a freezer (−2 to −6 °C) within 4 h of collection and kept frozen until 10 min prior to each presentation. Fecal samples were always presented individually and in random order (see details below) to single individuals in the morning, when meerkat groups are actively foraging. Samples were put on a 20 × 30 cm tray that was covered with locally collected sand before each presentation and placed in the foraging path of the recipient individual. The response to the fecal sample was recorded with a digital video camera (NV-GS500; Panasonic Corporation, Osaka, Japan) mounted on a tripod and positioned within 1 m of the presentation tray. We filmed the recipient individual from the moment it entered the field of view of the camera (45–60 cm around the tray) and inspected the fecal sample, until it resumed foraging or left the field of view and did not return to inspect the sample again for 1 min. In all of our experiments, recipient individuals were presented only once with each fecal sample type (see details below), and no more than 2 individuals per group were presented with samples within a same week to avoid habituation to the experiments.

Behavioral data collection

We recorded the time recipient individuals spent inspecting the fecal sample (nose within 1 cm of the sample), and the number of recruitment calls (Manser 2001) emitted and countermarks deposited in response to the sample. Counter marking included: anal marking (wiping the anal region across a surface), chew marking (biting vegetation), scuffing (frenzied digging), urinating, and defecating (Jordan 2007). We extracted the frequency and duration (to the nearest 0.02 s) of the behaviors of interest from the video recordings using the program fOCUS III (The Open University, Milton Keynes, and Psycle Interactive, London, United Kingdom). In addition to the behaviors recorded in the presence of the fecal sample, we conducted 10-min focal observations of the recipient individual after each presentation, once filming had concluded and the fecal sample had been removed. Time spent vigilant was recorded on a handheld computer (Organiser II LZ64; Psion Teklogix, London, United Kingdom), with times accurate to 1 s. Individuals were considered vigilant when they were bipedal or on raised guard (vigilant from a raised position, Clutton-Brock et al. 1999), with their gaze at the horizon. For experiment II, we conducted an additional focal observation before each presentation as a control, and we also recorded the time spent within 1 m of the dominant female, an indication of mate guarding (Jordan et al. 2007). We used the differences between post-presentation and control focal observation times in the analyses of these data.

Experiment I—sex and social status differences in responses

To determine first, whether meerkats respond differently to male scent marks from resident and foreign individuals

(intruders), and second, whether dominant males show stronger responses to intruder scent marks than individuals in all other sex and social status categories, fecal samples from resident males and foreign males were presented to the dominant and one adult subordinate individual of each sex in 8 meerkat groups. A sample from a randomly selected subordinate male from the recipient individual's own group, deposited while foraging with the group, was used as the resident sample. Foreign samples were collected from extra-group subordinate males while they were on prospecting forays. Potential differences among recipient individuals in their familiarity to the foreign sample donors were minimized by using fecal samples from males who themselves, and their groups had not encountered the recipient individual or its group within 6 months prior to their presentation. At the time of presentation, samples from resident and foreign males did not differ significantly in the number of days since deposition (resident: $\bar{x} = 25$ days, range 3–76; foreign: $\bar{x} = 35$ days, range 1–86; Wilcoxon signed-rank test: $Z = -1.66$, $P = 0.099$). Recipient individuals were presented with a sample of each type on the same day, with a 1-h interval between presentations.

A second series of presentations was conducted separately to verify that responses to the foreign samples were due to the donors being from a different group to that of the recipient rather than because the samples were collected while the donors were prospecting. An identical protocol was followed except that, in this case, the fecal sample deposited while prospecting was collected from a subordinate male from the recipient individual's own group. This same resident male also provided the control sample but deposited while foraging with its group. At the time of presentation, prospecting and control samples did not differ significantly in the number of days since deposition (prospecting: $\bar{x} = 42$ days, range 13–60; control: $\bar{x} = 41$ days, range 8–80; Wilcoxon signed-rank test: $Z = 0.36$, $P = 0.748$). Samples were presented to the dominant male and one randomly selected subordinate male in each of 5 groups.

Experiment II—temporal variation in response by dominant males

To determine whether dominant males increase their response to intruder scent marks when resident dominant females are in estrus, fecal samples from foreign subordinate males were presented to the dominant male in 9 meerkat groups during the estrus period (4–12 days after parturition, Jordan et al. 2007) and the observable period of pregnancy (40–60 days after conception, Clutton-Brock et al. 2008) of the dominant female. As dominant females can have up to 4 breeding attempts during a single breeding season (Russell et al. 2003), it was possible to randomize the order of the presentations. These multiple breeding attempts also allowed us to subsequently validate the postpartum estrus periods we designated, as all 9 dominant females in the groups used were visibly pregnant within 2 months after the estrus period presentations. Approximate conception dates for the 7 pregnancies carried to term, estimated by backdating 70 days (gestation period in meerkats, Clutton-Brock et al. 2008) from the day that dominant females gave birth, fell within our estrus windows. Fecal samples presented during the estrus period of the dominant female did not differ in days since deposition from those presented during pregnancy (estrus: $\bar{x} = 4$ days, range 1–10; pregnant: $\bar{x} = 5$ days, range 1–11; Wilcoxon signed-rank test: $Z = -0.54$, $P = 0.637$). We used samples from adult subordinate males that had prospecting at the focal dominant male's group at least once during the current breeding season to control for familiarity.

Statistical analyses

All statistical analyses were conducted using R 2.10.1 (R Development Core Team 2009), with lme4 (Bates and Maechler 2010) for fitting mixed models, coin (Hothorn et al. 2010) for Wilcoxon tests, and car (Fox 2009) for Box–Cox transformations. We analyzed data using Wilcoxon signed-rank tests when accounting for paired measures on the same individual or Fisher's exact tests for count data when behaviors were rare. When accounting for repeated measures of groups, we used general or generalized linear mixed models (LMM and GLMM) according to the distribution of the response variable. Initial mixed models included all potential explanatory variables and their interactions, which were then dropped in order of significance using a likelihood ratio test for model comparison, until minimal adequate models were achieved (Crawley 2007). Levels of significance and nonsignificance reported for explanatory terms were obtained by comparing minimal adequate models with models in which the term of interest had been added or removed. Post hoc comparisons were computed by dividing the differences between the parameter estimates from the minimal model by the standard error (SE) of the differences between them and interpreting the output as a *t*-test using the residual degrees of freedom (df) from the model (Zar 1999). A conservative approach was taken when calculating the residual df of a model by using the difference between the number of observations and the maximum possible number of df associated with both random and fixed terms (Baayen et al. 2008).

To investigate the differences in responses to resident and foreign male feces (experiment I), separate mixed models were used for each of the response variables, with fecal sample type (resident or foreign) and its 2- and 3-way interactions with sex and social status of the recipient individual included as explanatory variables. Age of the donor of the fecal sample varied between the 2 sample types (resident: $\bar{x} = 531$ days of age, range 291–1090; foreign: $\bar{x} = 900$ days of age, range 335–1374; Wilcoxon signed-rank test: $Z = -4.23$, $P < 0.001$) and was therefore fitted as a fixed effect in these models, along with order in which the sample was presented (first or second) and its interaction with sample type. One of our response variables, number of recruitment calls emitted, was zero-inflated and was therefore analyzed using 2 models. First, a binary model determined whether there were differences in the presence or absence of the response behavior between presentations of resident and foreign samples and among categories of individual. We used a quasi-GLMM approach to account for the overdispersion detected in this first model with binomial error structure (Zuur et al. 2009). A second model included data only from individuals that emitted recruitment calls to at least one of the samples presented ($n = 17$), to determine whether the differences from the number of recruitment calls emitted in response to the foreign sample minus the number emitted in response to the resident sample, differed among categories.

RESULTS

Sex and social status differences in responses to intruder scent marks

For all individuals tested, the likelihood of emitting recruitment calls was affected by an interaction between the sample type presented and the order of presentation, with the highest probability of emitting recruitment calls occurring when foreign fecal samples were presented first (Table 1a). The greatest difference in probabilities of emitting recruitment calls between sample types occurred when the foreign sample was presented first (Figure 1), but post hoc comparisons revealed

Table 1

Factors influencing an individual's (a) probability of emitting recruitment calls, (b) difference in number of recruitment calls emitted (foreign–resident), and (c) time spent inspecting samples, during presentations of fecal samples

Response term	Explanatory terms	Estimate ± SE	<i>t</i>	<i>P</i>
(a) Recruitment calls (yes, no)	(Intercept)	−3.53 ± 0.42	−8.35	
	Sample type × order	Foreign × 2nd: −4.02 ± 0.53 (see Figure 1)	−7.53	0.003
	Sample type	Foreign: +3.74 ± 0.44	8.49	
	Order	2nd: +1.99 ± 0.43	4.63	
	Sex	Male: +1.33 ± 0.24	5.48	0.040
	Social status			0.999
(b) Difference in number of recruitment calls (square root)	(Intercept)	+1.05 ± 0.57	1.84	
	Sex × social status	Male × sub.: −1.52 ± 0.71 (see Figure 2)	−2.13	0.027
	Sex	Male: +2.92 ± 0.64	4.55	
	Social status	Subordinate: +0.70 ± 0.56	1.25	
	Donor age diff.	−0.00 ± 0.00	−2.01	0.030
	Order			0.661
(c) Time spent inspecting sample (Box–Cox transformed)	(Intercept)	+1.05 ± 0.01	80.91	
	Sample type × sex	Foreign × male: +0.05 ± 0.02 (see Figure 3)	2.58	0.010
	Sample type	Foreign: +0.03 ± 0.01	1.79	
	Sex	Male: +0.03 ± 0.01	1.94	
	Order	2nd: −0.03 ± 0.01	−2.70	0.007
	Social status			0.605
Donor age			0.895	

Shown are the results of LMMs and a GLMM fitted with group identity as a random term. Individual identity was also fitted as a random term in (a) and (c). Quasi-binomial errors were used for (a). Explanatory terms and interactions highlighted in bold were included in the minimal models.

that differences in probabilities were significant when it was presented second as well (foreign first $t = 5.94$, $df = 20$, $P < 0.001$; resident first $t = 3.90$, $df = 20$, $P < 0.001$). Dominant males showed the greatest difference in the number of recruitment calls emitted between presentations of resident and foreign samples, whereas dominant females showed the least (sex and social status interaction: Table 1b; Figure 2). Other group members approached the recipient individual in response to its recruitment calls on 5 occasions, in all of which a foreign fecal sample had been presented. The approaches occurred in response to the highest numbers of recruitment calls emitted (range 6–21), regardless of the identity of the caller. In terms of sample inspection time, there was a signifi-

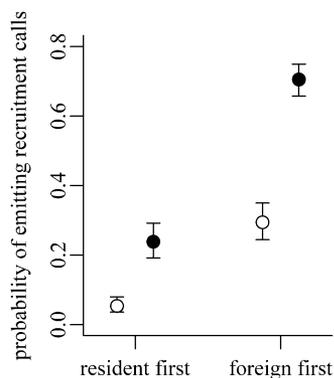


Figure 1

Effect of the interaction between sample type and order in which samples were presented on the probability that an individual ($n = 31$) emitted at least one recruitment call during the presentation of a fecal sample (resident: open circle; foreign: filled circle). Circles show the mean of predicted values for females ($n = 15$) and males ($n = 16$) from the GLMM in Table 1a (± 1 SE, both converted to the original scale).

cant interaction between the type of sample presented and the sex of the recipient (Table 1c, Figure 3). Males, regardless of social status, spent significantly more time inspecting the foreign sample than the resident one, whereas females did not (LMM post hoc comparison: males $t = 5.57$, $df = 20$, $P < 0.001$; females $t = 1.79$, $df = 20$, $P > 0.05$). Males also inspected the foreign samples for longer than females (LMM post hoc comparison: $t = 5.50$, $df = 20$, $P < 0.001$). Dominant males were the only individuals who deposited countermarks and only did so when the sample presented was from a foreign male (5 of 8 cases, compared with 0 for each of the other 3 categories of individual; Fisher's exact test: $P = 0.001$). Dominant males used anal marks, urine, chewing, and scuffing as countermarks, which were placed near but never directly on top (i.e., overmark) of the foreign fecal sample ($\bar{x} = 1.5$

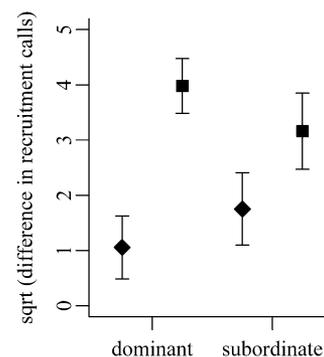


Figure 2

Effect of the interaction between sex and social status of the recipient on the difference in number of recruitment calls emitted between sample types presented (foreign–resident) for dominant and subordinate females (diamonds; n dominant = 3; n subordinate = 4) and males (squares; n dominant = 5; n subordinate = 5). Symbols show predicted values from the LMM in Table 1b (± 1 SE).

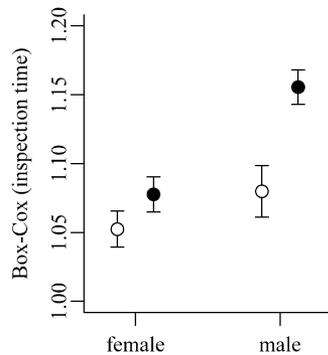


Figure 3
Effect of the interaction between sample type and sex of the recipient on the time females ($n = 15$) and males ($n = 16$) spent inspecting the fecal sample presented (resident: open circle; foreign: filled circle). Circles show predicted values from the LMM in Table 1c (± 1 SE).

countermarks, range 0–5). There was no difference in the proportion of time individuals spent vigilant in the 10 min after presentations were conducted, between presentations of resident and foreign fecal samples (LMM: sample type: $t = 1.15$, $P = 0.256$).

Males showed no difference in their responses to feces of males from their own group, regardless of whether the sample presented had been collected while the donor was foraging with its group or prospecting. There were no differences between the sample types presented in the time spent inspecting the feces ($Z = 0.15$, $P = 0.922$), number of recruitment calls emitted ($Z = 1.01$, $P = 0.312$), or proportion of samples countermarked (one dominant male countermarked both samples) by recipient males ($n = 10$).

Temporal variation in response to intruder scent marks by dominant males

Dominant males spent less time inspecting the foreign samples presented when the resident dominant female was in estrus than when pregnant ($Z = 2.31$, $P = 0.020$; Figure 4a), but there was no difference in number of recruitment calls emitted ($Z = 0.84$, $P = 0.453$; Figure 4b). Dominant males only countermarked the sample presented when the dominant female was pregnant ($\bar{x} = 1.4$ countermarks, range 0–7), but the proportion of individuals that countermarked (4 of 9) was not significantly different from zero (Fisher's exact test:

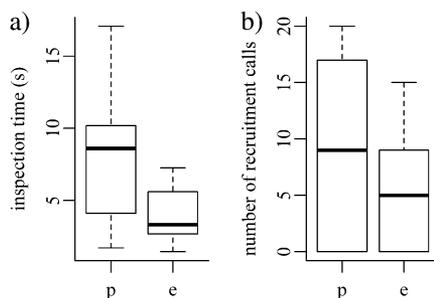


Figure 4
Influence of the resident dominant female's reproductive status (p: pregnant; e: estrus) on (a) the time spent inspecting the fecal samples and (b) the number of recruitment calls emitted by dominant males ($n=9$) during presentations. Boxplots show the median (line within boxes), 25 and 75% quartiles (lower and upper ends of boxes), and 1.5 times the interquartile range (dashed lines) of the data.

$P = 0.082$). There were no significant differences between the 2 reproductive phases in the proportion of time dominant males spent vigilant ($Z = 1.48$, $P = 0.164$) or mate guarding ($Z = -0.95$, $P = 0.391$) after the presentations. When comparing only among control focal observations for each behavior, there were no differences between pregnant and estrus period observations (vigilance: $Z = -0.77$, $P = 0.496$; mate guarding: $Z = 1.54$, $P = 0.148$).

DISCUSSION

Meerkats showed distinct responses to feces from extragroup males compared with those from resident males, in accordance with empirical and experimental studies on scent mark discrimination in other group-living carnivores (e.g., European badger, *Meles meles*: Buesching et al. 2002; banded mongoose: Müller and Manser 2007; and spotted hyena, *Crocuta crocuta*: Burgener et al. 2008). Dominant males had the strongest response to intruding male scent marks, consistent with the idea that intense reproductive conflict with extragroup individuals predicts strong responses to intruders of the same sex. The increased alarm behavior to intruder scent marks across all categories of individual suggests that other group members may also participate in repelling intruders, for reasons other than mate defense. Although sex (Gosling and Roberts 2001; Palagi and Dapporto 2007) and social status (Thiessen and Rice 1976; Hurst 1990) are known to affect responses to intruder scent marks, our results are the first to show detailed differences in individual responses to intruder scent marks in a cooperative breeder with high reproductive skew.

Individuals of all sex and social status combinations were more likely to emit recruitment calls when presented with feces from intruders than with resident male feces, supporting previous observations that meerkats respond to encounters with foreign scent marks by emitting recruitment calls (Manser 2001). We interpret these calls as a correlate of response intensity to a perceived threat, as similar alarm-like vocalizations are emitted by meerkats when encountering secondary cues from predators (Manser 2001) and are also used by banded mongooses in similar contexts (Cant et al. 2002; Müller and Manser 2008). This general response may seem to conflict with the idea that the defense of breeding opportunities is the primary reason for strong responses to intruders. However, as well as affecting the reproductive success of dominant males, extragroup males may increase the reproductive conflict between dominant and subordinate females (Clutton-Brock et al. 2001; Griffin et al. 2003) and can reduce the inclusive fitness of all resident subordinates by reducing their relatedness to the young they help rear. Alternatively, all individuals may be alarming initially to the presence of a foreign scent, without knowing if the intruder is a single individual or a whole group. Intruding groups can be a serious threat to all resident individuals, through the potential loss of territory and, when pups are present in the group (in all but 6 of the presentations in experiment I), through infanticide (Young 2003). As meerkats respond to recruitment calls by joining the caller (Manser 2001), alarming at intruder scent marks may ultimately distribute the costs of defending a group's resources.

Unlike dominant and subordinate females, all male meerkats spent significantly more time inspecting the foreign fecal samples than the resident male samples. This is in contrast to the absence of sex-specific responses to intruder scents suggested in badgers (Palphramand and White 2007), a species where extragroup mating is also common (Dugdale et al. 2007). Palagi and Dapporto (2007) suggested that dimorphism in responses to scent cues reflects differences in motivation and territorial defense, which should be influenced by

the perceived level of threat that an intruder poses to a resident individual. Intruding males in big enough coalitions relative to the number of resident males may take over established breeding groups, expelling all males in the process (Young 2003). Resident males are thus expected to respond more aggressively to same-sex intruders, as has been suggested in meerkats (Doolan and Macdonald 1996; Young et al. 2005) and in many other mammal species (e.g., lion: Heinsohn et al. 1996; spotted hyena: Boydston et al. 2001; common marmoset: Lazaro-Perea 2001; and banded mongoose: Cant et al. 2002). Detecting and identifying extragroup males through their scent marks could allow resident males to quickly identify intruders later on through scent matching (Gosling 1982; Hurst and Beynon 2004). This may benefit resident males by eliminating the need to inspect the intruders themselves, thus reducing the time needed to respond to intruder approaches appropriately.

The strongest response to intruding male scent marks was observed in dominant males, who showed the highest increase in number of recruitment calls emitted and were the only ones to countermark when presented with the foreign fecal samples. Dominant individuals in other social species also countermark same-sex intruder scent marks more frequently than subordinates (Thiessen and Rice 1976; Hurst 1990), potentially as a reaffirmation of competitive ability and commitment to defend resources (Hurst and Beynon 2004). Our results are in sharp contrast with those reported for banded mongooses, however, where all resident males countermark scent marks deposited by male group members, reflecting the high within-group reproductive conflict (Müller and Manser 2008). A previous study on meerkat latrine behavior found that dominant and subordinate males deposit scent marks and overmark female scent marks from their own group at similar rates, potentially as a form of both territory and mate defense (Jordan 2007). We suggest that the absence of countermarking (and overmarking) by subordinate males and the preferential countermarking of foreign over resident feces by dominant males in our study, support the idea that mate defense may be the primary motivation for countermarking intruding male scent marks.

Given that males may be adjusting their responses to other males according to levels of reproductive conflict, it is perhaps surprising that dominant males did not increase the intensity of their response to intruder feces when dominant females were most receptive. On the contrary, dominant males significantly reduced the time they invested inspecting fecal samples and never countermarked the fecal sample presented when the resident dominant female was in estrus. Kutsukake and Clutton-Brock (2008) argued that intense mate guarding during the estrus period of the dominant female imposed time and energy constraints on dominant males, which could explain our results. However, we did not find any differences in the time dominant males spent mate guarding during pre-presentation (control) focal observations, between the 2 reproductive phases of the dominant female. It is possible that dominant males are in fact mate guarding, hence, the reduction in time spent inspecting the samples during estrus, but our measure of mate guarding may have been too restrictive. As meerkats are active during the day and typically forage in open areas, effective mate guarding may not require that a dominant male remain in close proximity to the dominant female. The absence of an increase in or the complete lack of countermarking by dominant males during the dominant female estrus period in our study, could be due to limitations on scent mark production (e.g., feces: Brashares and Arcese 1999; urine: Hurst and Beynon 2004) and to shifts in male scent-marking priorities. Within meerkat groups, males selectively overmark female scent marks, which has been suggested

as a way of masking the presence of females from extragroup males (Jordan 2007). If as in other species (e.g., Alaskan moose, *Alces alces gigas*: Bowyer et al. 1994; meadow vole, *Microtus pennsylvanicus*: Ferkin et al. 2004; and ringtailed lemur, *Lemur catta*: Scordato and Drea 2007), female meerkats increase their rates of scent marking during estrus, dominant males may be under increased demand to overmark female scent marks, which could impede any increase in countermarking rates of intruder feces. Further research on female scent-marking behavior and its potential effect on male countermarking patterns are warranted.

In conclusion, we found experimental evidence that meerkats of all sex and social status respond differently to intruding male than to resident male feces. In accordance with the sex-specific responses to intruders observed in other species, we also showed that resident males spent more time inspecting intruder feces than resident feces, but females did not. Moreover, among males, social status was important in determining the response intensity toward intruding male feces. We found that dominant males had the strongest overall response to intruding male feces, as predicted by the potentially high level of reproductive conflict between resident dominant and subordinate extragroup males, but investment in some of these response behaviors may in fact decrease when females are most receptive. Although we did not test resident individuals' responses to scent marks of all types of territorial intruders (e.g., prospecting male coalitions, foreign groups), our results suggest that, in cooperatively breeding species, all members of a group may participate in resource defense, but sex and social status may affect an individual's investment in deterring male intruders.

FUNDING

Instituto para la Formación y Aprovechamiento de Recursos Humanos and the Secretaría Nacional de Ciencia, Tecnología e Innovación scholarship program (270-2007-339 to R.M.).

We thank the management team and the volunteers at the Kalahari Meerkat Project for providing logistical support and invaluable assistance with data and sample collection. We are grateful to the Kotze family for allowing us to work on their land and to the Northern Cape Conservation Authority for granting us permission to conduct research on meerkats in the Kalahari. We would also like to thank A. Bateman for his help with statistical analyses, and S. English, S. Sharp, and 2 anonymous reviewers for their comments that greatly improved the original manuscript.

REFERENCES

- Baayen RH, Davidson DJ, Bates DM. 2008. Mixed-effects modeling with crossed random effects for subjects and items. *J Mem Lang*. 59:390–412.
- Bates D, Maechler M. 2010. lme4: linear mixed effects models using S4 classes. R package version 0.999375-33 [cited 2011 March 07]. Available from: <http://cran.r-project.org/web/packages/lme4/index.html>.
- Bowyer RT, Vanballenberghe V, Rock KR. 1994. Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. *Can J Zool*. 72:2186–2192.
- Boydston EE, Morelli TL, Holekamp KE. 2001. Sex differences in territorial behavior exhibited by the spotted hyena (*Hyaenidae*, *Crocuta crocuta*). *Ethology*. 107:369–385.
- Brashares JS, Arcese P. 1999. Scent marking in a territorial African antelope: II. The economics of marking with faeces. *Anim Behav*. 57:11–17.
- Buesching CD, Waterhouse JS, Macdonald DW. 2002. Gas-chromatographic analyses of the subcaudal gland secretion of the European badger (*Meles meles*) part I: chemical differences related to individual parameters. *J Chem Ecol*. 28:41–56.

- Burgener N, East ML, Hofer H, Dehnhard M. 2008. Do spotted hyena scent marks code for clan membership? In: Hurst JL, Beynon RJ, Roberts SC, Wyatt TD, editors. Chemical signals in vertebrates 11. New York: Springer Science+Business Media, LLC. p. 169–177.
- Cant MA, Otali E, Mwanguhya F. 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology*. 108:541–555.
- Carlson AA, Young AJ, Russell AF, Bennett NC, McNeilly AS, Clutton-Brock TH. 2004. Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Horm Behav*. 46:141–150.
- Clutton-Brock TH, Brotherton PNM, Russell AF, O’Riain MJ, Gaynor D, Kansky R, Griffin A, Manser M, Sharpe L, McIlrath GM, et al. 2001. Cooperation, control, and concession in meerkat groups. *Science*. 291:478–481.
- Clutton-Brock TH, Hodge SJ, Flower TP. 2008. Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Anim Behav*. 76:689–700.
- Clutton-Brock TH, O’Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser M. 1999. Selfish sentinels in cooperative mammals. *Science*. 284:1640–1644.
- Cooney R. 2002. Colony defense in Damaraland mole-rats, *Cryptomys damarensis*. *Behav Ecol*. 13:160–162.
- Crawley MJ. 2007. The R book. Chichester (UK): John Wiley & Sons Ltd.
- Doolan SP, Macdonald DW. 1996. Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *J Zool*. 240:59–73.
- Dugdale HL, Macdonald DW, Pope LC, Burke T. 2007. Polygyny, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. *Mol Ecol*. 16:5294–5306.
- Emlen ST. 1991. Evolution of cooperative breeding in birds and mammals. In: Krebs J, Davies NB, editors. Behavioural ecology: an evolutionary approach. Oxford: Blackwell Scientific Publications. p. 301–337.
- Ferkin MH, Lee DN, Leonard ST. 2004. The reproductive state of female voles affects their scent marking behavior and the responses of male conspecifics to such marks. *Ethology*. 110:257–272.
- Fox J. 2009. car: Companion to Applied Regression. R package version 1.2-16 [cited 2011 March 07]. Available from: <http://cran.r-project.org/web/packages/car/index.html>.
- Gosling LM. 1982. A reassessment of the function of scent marking in territories. *Z Tierpsychol*. 60:89–118.
- Gosling LM, Roberts SC. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Adv Study Behav*. 30:169–217.
- Griffin AS, Pemberton JM, Brotherton PNM, McIlrath G, Gaynor D, Kansky R, O’Riain J, Clutton-Brock TH. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav Ecol*. 14:472–480.
- Heinsohn R, Packer C, Pusey AE. 1996. Development of cooperative territoriality in juvenile lions. *Proc R Soc Lond B Biol Sci*. 263:475–479.
- Hothorn T, Hornik K, van de Wiel M, Zeileis A. 2010. coin: Conditional Inference Procedures in a Permutation Test Framework. R package version 1.0-17 [cited 2011 March 07]. Available from: <http://cran.r-project.org/web/packages/coin/index.html>.
- Hurst JL. 1990. Urine marking in populations of wild house mice *Mus domesticus* Ruddy. I. Communication between males. *Anim Behav*. 40:209–222.
- Hurst JL, Beynon RJ. 2004. Scent wars: the chemobiology of competitive signalling in mice. *BioEssays*. 26:1288–1298.
- Johansson BG, Jones TM. 2007. The role of chemical communication in mate choice. *Biol Rev*. 82:265–289.
- Johnson RP. 1973. Scent marking in mammals. *Anim Behav*. 21:521–535.
- Jordan NR. 2007. Scent-marking investment is determined by sex and breeding status in meerkats. *Anim Behav*. 74:531–540.
- Jordan NR, Cherry MI, Manser MB. 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Anim Behav*. 73:613–622.
- Kutsukake N, Clutton-Brock TH. 2008. The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats. *Proc R Soc B Biol Sci*. 275:209–216.
- Lazaro-Perea C. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Anim Behav*. 62:11–21.
- Manser MB. 2001. The acoustic structure of suricates’ alarm calls varies with predator type and the level of response urgency. *Proc R Soc Lond B Biol Sci*. 268:2315–2324.
- Müller CA, Manser MB. 2007. “Nasty neighbours” rather than “dear enemies” in a social carnivore. *Proc R Soc B Biol Sci*. 274:959–965.
- Müller CA, Manser MB. 2008. Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology*. 114:174–185.
- O’Riain MJ, Jarvis JUM. 1997. Colony member recognition and xenophobia in the naked mole-rat. *Anim Behav*. 53:487–498.
- Palagi E, Dapporto L. 2007. Females do it better. Individual recognition experiments reveal sexual dimorphism in *Lemur catta* (Linnaeus 1758) olfactory motivation and territorial defence. *J Exp Biol*. 210:2700–2705.
- Palphramand KL, White PCL. 2007. Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. *Anim Behav*. 74:429–436.
- R Development Core Team. 2009. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited 2011 March 07]. Available from: <http://www.R-project.org>.
- Russell AF, Brotherton PNM, McIlrath GM, Sharpe LL, Clutton-Brock TH. 2003. Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behav Ecol*. 14:486–492.
- Russell AF, Clutton-Brock TH, Brotherton PNM, Sharpe LL, McIlrath GM, Dalerum FD, Cameron EZ, Barnard JA. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. *J Anim Ecol*. 71:700–709.
- Scordato ES, Drea CM. 2007. Scents and sensibility: information content of olfactory signals in the ringtailed lemur, *Lemur catta*. *Anim Behav*. 73:301–314.
- Spong GF, Hodge SJ, Young AJ, Clutton-Brock TH. 2008. Factors affecting the reproductive success of dominant male meerkats. *Mol Ecol*. 17:2287–2299.
- Thiessen D, Rice M. 1976. Mammalian scent gland marking and social behavior. *Psychol Bull*. 83:505–539.
- Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim Behav*. 61:1203–1216.
- Wyatt TD. 2003. Pheromones and animal behaviour: communication by smell and taste. Cambridge: Cambridge University Press.
- Young AJ. 2003. Subordinate tactics in cooperative meerkats: helping, breeding and dispersal. Cambridge: University of Cambridge. [PhD thesis].
- Young AJ, Carlson AA, Clutton-Brock TH. 2005. Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Anim Behav*. 70:829–837.
- Young AJ, Spong G, Clutton-Brock TH. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proc R Soc B Biol Sci*. 274:1603–1609.
- Zar JH. 1999. Biostatistical analysis. Upper Saddle River (NJ): Prentice Hall.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Statistics for biology and health. New York: Springer Science+Business Media.