Original Article

Rival group scent induces changes in dwarf mongoose immediate behavior and subsequent movement

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In many social species, groups of animals defend a shared territory against rival conspecifics. Intruders can be detected from a variety of cues, including fecal deposits, and the strength of response is expected to vary depending on the identity of the rival group. Previous studies examining differences in response to neighbor and stranger groups have focused on the immediate response to the relevant cues. Here, we investigated how simulated intrusions of rival groups affect both immediate responses and postinspection movement patterns. To do so, we used a fecal translocation experiment at latrine sites within the territories of dwarf mongoose *Helogale parvula* groups. Immediate responses were adjusted to the level of threat, with greater scent-marking behavior, time spent at the latrine, and group-member participation when groups were presented with fecal matter from out-group rivals relative to control (own group and herbivore) feces. Subsequent movement of the group was also affected by threat level, with a decrease in speed and distance covered following simulated intrusions by out-group rivals compared with control conditions. However, there were no significant differences in immediate responses or post-latrine movement patterns when comparing simulated neighbor and stranger intrusions. These results indicate that territorial intrusions can elicit not just an immediate change in behavior but more far-reaching consequences in terms of movement dynamics. They also raise the possibility that neighbor–stranger discrimination predictions are not necessarily as clear-cut as previously described.

Key words: **group identity, identity cues, latrine behavior, out-group conflict, social behavior, territory defense.**

INTRODUCTION

In many social species across a range of animal taxa, individuals form stable groups that collectively defend a territory against conspecifics (Taborsky 1984; Radford 2003; Kitchen and Beehner 2007; Batchelor and Briffa 2011). The level of threat posed by rival groups is likely dependent on several factors. For instance, the territorial location can be important, with intruders nearer the center than the periphery or those close to particularly valuable resources perceived as a greater threat (Furrer et al. 2011; Brown 2013). Relative resource-holding potential can also have an influence, with larger groups tending to dominate smaller ones in intergroup conflicts (McComb et al. 1994; Radford and du Plessis 2004). Moreover, intruder identity can affect the degree of threat, with differences in response to neighbors and strangers found in a number of taxa (Temeles 1994).

The "dear-enemy phenomenon" (Fisher 1954), where residents show less aggressive responses to intruding neighbors compared with strangers, is found in some group-living species such as green woodhoopoes *Phoeniculus purpureus* (Radford 2005). In general, neighbors might be less threatening than strangers either because they are known to be continuously present at a mutual border, whereas intrusions by strangers are spatially and temporally unpredictable (Jordan et al. 2007), or because they already own a territory, whereas transient strangers may be looking to usurp residents and take over (Wilson 1980). The "nasty-neighbor phenomenon" (Müller and Manser 2007), where intrusions by neighbors are countered with higher levels of aggression than those by strangers, is found in other group-living species such as banded mongooses *Mungos mungo*, where emigration from the natal territory is undertaken in small groups (Müller and Manser 2007). Small stranger groups pose less threat to established residents than large neighboring groups both in terms of size and intention: Stranger groups might simply be passing through, whereas neighbors could be seeking to expand their territory (Mech and Boitani 2003; Müller and Manser 2007).

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Neighbor–stranger discrimination (NSD) has been shown to be possible through vocal, visual, and olfactory cues. Resident green woodhoopoes responded significantly more rapidly to playbacks of strangers (posing the threat of permanent territorial eviction) than of neighbors (causing temporary displacements) (Radford 2005), whereas other species even discriminate between different neighboring groups based on their vocalizations (e.g., vervet monkeys *Cercopithecus aethiops*, Cheney and Seyfarth 1980; chimpanzees *Pan troglodytes*, Crockford et al. 2004). In Jacky dragons *Amphibolurus muricatus*, static presentations of unfamiliar individuals elicited significantly higher levels of arousal and signs of information gathering than familiar individuals, supporting dear-enemy predictions (Husak 2004; Van Dyk and Evans 2007). Eurasian beavers *Castor fiber*, European badgers *Meles meles*, and African wild dogs *Lycaon pictus* all responded more intensely to scent-marks from strangers than to those from neighbors (Rosell 2001; Palphramand and White 2007; Parker 2010), whereas banded mongooses responded more strongly when encountering the scent of a neighbor than of a stranger group (Müller and Manser 2007).

To date, studies of how residents respond to intruder scent-marks have focused on the immediate behavioral responses. Inspection, over-marking (i.e., depositing own scent over the encountered scent), and physical displacement or destruction of the scent-mark, as well as the number of individuals participating and vocalizations given to recruit other group members, have all been shown to vary depending on the level of perceived threat (Roper et al. 1993; Rosell 2001; Müller and Manser 2007; Mares et al. 2011). However, the discovery of intruder scent-marks might also be expected to influence subsequent behavior, as is the case following actual encounters between rival groups. For instance, white-faced capuchin monkeys *Cebus capucinus* traveled further, faster, and more linearly if a conflict was lost (Crofoot 2013); increased speed incurs energetic costs and faster travel means a smaller likelihood of detecting food (Janson and Di Bitetti 1997) and less time spent resting (Dunbar RIM and Dunbar P 1988). Straight-line movement has been associated with flight (e.g., coyotes *Canis latrans*, Neale et al. 2007), whereas increased tortuosity could indicate a search pattern (e.g., Weddell's saddleback tamarins *Saguinus fuscicollis weddelli*, Porter and Garber 2013). Territory exploration (visiting sleeping burrows) after the detection of a transient group scent-mark has been noted in meerkats *Suricata suricatta* (Jordan et al. 2007), but movement patterns after the detection of intruder scent-marks has yet to be addressed experimentally in a group-living species.

In this study, we use dwarf mongooses *Helogale parvula* to investigate immediate and longer-term responses to simulated territorial intrusions (feces placed within the focal territory) by rival conspecific groups. Dwarf mongooses live in cooperatively breeding groups with a dominant breeding pair; group members sleep, forage, and travel together within a shared territory (Rood 1983; Kern and Radford 2013). Cooperative territorial behavior involves scent-marking at communal latrines and physical defense when other groups are encountered (Rasa 1973). Four olfactory channels are used: urine, fecal matter, and both cheek gland and anal gland secretions (Rasa 1973). In a captive setting, the introduction of fecal matter from an unfamiliar pair resulted in increased anal gland marking by a focal pair compared with when their own fecal matter was present (Rasa 1973). Recent findings in the field suggest that no discrimination is made between stranger and own fecal matter when single feces are presented alongside one another (Sharpe 2015). However, latrines in the wild are usually frequented as a group and scent-marks are deposited by multiple group members

at such sites (Sharpe et al. 2012), likely resulting in a group signature (Ewer 1968; Rasa 1973). We therefore investigated group-level responses to out-group threats as indicated by feces from several individuals.

Our fecal-presentation experiment, considering both immediate behavioral interactions with the presented feces and subsequent movement patterns by the territory-holding group, aimed to answer 2 main questions. First, do territory holders respond more strongly to feces from other groups (out-group threat) than to control feces (those from their own group and from herbivores)? Because out-group feces will be less familiar to individuals than those from their own group, and out-groups represent a potential threat in terms of resource loss and territory usurpation, we predicted a stronger response to feces from rival groups compared with control feces. Second, do territory holders respond differentially to feces from neighbors and strangers? Neighboring dwarf mongoose groups commonly contest the temporary rights to sleeping burrows on the mutual boundary of their territory, whereas conflict with transient groups rarely involves sleeping-site contestation and are generally less intense (Rasa 1987). The majority of observed intergroup interactions take place between neighboring groups (Kern J, Christensen C, unpublished data) and repeated intrusions intensify responses to rivals in other species (Monclús et al. 2014). We therefore predicted a stronger response to feces from neighbors than to those from strangers.

MATERIAL AND METHODS
Study site and population

The study was conducted on Sorabi Rock Lodge, a 4 km² private reserve in the Limpopo Province, South Africa (24°11′S, 30°46′E), part of southern Africa's Savannah Biome (see Kern and Radford 2013 for full details). We collected data over 2 periods: November 2013–January 2014 (summer) and June 2014–October 2014 (winter). All procedures were approved by the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UB11/038).

The long-term study population consists of 8 groups of dwarf mongooses (group sizes ranging from 3 to 15 individuals), habituated to close human presence on foot and thus allowing for detailed observation (<5 m) in natural conditions (Kern and Radford 2013, 2014). Individuals can be identified from marks of blond hair-dye (Garnier Nutrisse) applied using an elongated paint-brush while distracting the mongoose with egg. Dominant individuals are recognized by their higher levels of aggression, feeding displacement, and greeting behaviors (Rasa 1977; Kern et al. 2016). Groups are visited regularly to maintain habituation, reapply hair-dye, collect baseline data, and keep track of important life-history events (e.g., pregnancies, births, emigration, dominance changes, and deaths).

Experimental protocol

The experiment aimed to investigate differences in both immediate behavioral responses and subsequent movement patterns following 4 different fecal presentations. The 4 treatments comprised feces collected from: a neighboring group (Neighbor), a non-neighboring group (Stranger), the focal group (Own), and a herbivore (Herbivore). Own and Herbivore represent 2 forms of control: Own controlled for the presence of conspecific fecal matter, which might be expected to result in some responses due to intragroup nonterritorial functions (Rasa 1973; Sharpe 2015), and Herbivore

controlled for the interference by the experimenter with the latrine and the addition of feces. We presented treatments to the same group on different days in a randomized order; subsequent analysis confirmed that there was no unintentional bias in the ordering of different treatments (Friedman test: $\chi^2 = 2.35$, $n = 13$, $P = 0.502$).

To standardize between the different mongoose fecal treatments (Own, Neighbor, Stranger), each presented sample consisted of 1 feces from each of 4 separate group members, including at least one of the dominant pair. For the Herbivore treatment, we used 4 fecal pellets from greater kudu *Tragelaphus strepsiceros* or giraffe *Giraffa camelopardalis* (diameter ~2 cm; same size as dwarf mongoose feces). Feces were collected within 5 min of deposition, placed in airtight, sealed plastic bags inside glass pots while in the field, and stored overnight in a fridge (5 °C). Feces were always used in an experimental presentation within 1 day of collection (mean ± standard error [SE] = 13.0 ± 1.6 h), and there was no significant difference between treatments in time between collection and use (Friedman test: $\chi^2 = 1.92$, $n = 13$, $P = 0.584$).

We conducted fecal presentations at mongoose latrines, which are communal, frequently used elimination sites. Latrines are recognizable by the accumulation of fecal matter (Rasa 1973), and their location was marked using handheld GPS devices (Garmin Etrex H GPS; Garmin Europe Ltd, Southampton, Hampshire, UK) during observational data-collection sessions. After the focal group left their sleeping burrow, the observer tracked the presence of nearby latrines using the GPS map while following the foraging group. If the group was approaching a latrine (within 15 m), the observer moved ahead quietly and placed the fecal presentation on the ground at that site, before moving 5 m away; this distance allowed detailed observations without affecting latrine activity by the mongooses. We did not conduct fecal presentations if there had been an intergroup interaction earlier in the day; at least 30 min were allowed to elapse after any other latrine activity before feces were presented in an experimental trial.

Data collection

We defined the start of the focal-group response as the first interaction (sniffing) with the fecal presentation by any group member. Thereafter, we recorded the following data: number and identity of individuals present at the latrine (every 30 s); the total time spent at the latrine by all responders; and the latrine behaviors exhibited (sniffing, urinating, defecating, cheek gland marking, and anal gland marking by handstanding) by all responders. Cheek gland marking involves rubbing the corners of both cheeks alternately against a surface, is predominantly performed by dominant individuals, and is considered a display of aggression. Anal gland marking is performed by everting the anal gland pouch containing anogenital secretions; adopting a "handstand" position, balancing on the forelegs, and swinging the back legs up to mark sloping surfaces allows individuals to deposit the scent at an elevated level (Rasa 1973; Estes 1999). We gave each latrine behavior in the 15 min following the first interaction with the fecal presentation a score, based on its rank inferred from assumed energy investment and importance in territorial defense; anal gland marking by handstanding is considered the most energetically costly scent-marking behavior (Sharpe et al. 2012): sniffing = 1, urinating = 2, defecating = 3, cheek gland marking = 4, anal gland marking = 5. We summed scores to generate a "response level" value for the group.

We collected continuous movement data (track position recorded every 10 s) using a GPS for the hour after the interaction with the fecal presentation. We imported data via Basecamp (software

version 4.4.6, Garmin Ltd) into Mapsource (software version 6.16.3, Garmin Ltd) and stored them as daily movement maps. From these maps, the distance traveled, time of travel, average speed, and the area covered by the track were calculated automatically. To infer "directness" of travel, we calculated circuity indexes by dividing the track distance by the direct distance between the location of the fecal presentation and the location of the group 1 h after the first interaction (Janson 1998; Porter and Garber 2013).

Assignment of latrine locations

Although the initial aim was to conduct all fecal presentations in the periphery of the territory—territory location is known to influence the response to intruders in other group-living species (Furrer et al. 2011; Brown 2013)—this was precluded by the limited range used by our study population during the data-collection period in the second field season. To classify each experimental latrine site as either core or periphery, we calculated home ranges using the movement data collected over the 6 months preceding the relevant experimental field season. In the 2 instances where prior movement data did not extend back 6 months, we used all available data (3 months in both cases). Six months were chosen as a balance between including sufficient data (mean ± SE observation sessions = 50.5 ± 3.8; mean ± SE geographical data points = 480 ± 60) and delineating a plausible home range, as space use varies over time (Kern J, unpublished data). We transferred the geographical waypoint data from the daily movement maps for each group during each period into Mapsource (as above) and then into QGIS (version 2.6.1 Brighton, FOSS). Using the minimum convex polygon (MCP) algorithm from the plugin AniMove (version 6.16.14, Garmin Corp), we calculated MCPs using 100% of the data point fixes to estimate the full home range (as in Gilchrist and Otali 2002; Mattisson et al. 2013). Subsequently, the central 50% fixes were used to determine which latrines were classified as core (within MCP 50) and which as peripheral (outside MCP 50) (as in José and Lovari 1998; Jędrzejewski et al. 2007).

Data analysis

We analyzed data using R version 3.1.2 (R Development Core Team 2012). We used mixed models to take account of repeated data from the same group. Linear mixed models were used throughout because datasets, or their log or square-rooted transformations, fit the assumptions of parametric testing. We added treatment (Neighbor, Stranger, Own, Herbivore), territorial location (Core, Periphery), pup presence (Yes, No), and time of day (AM, PM) as fixed effects. Pup presence was defined as the period of time after birth until the pups are observed to first forage independently (~1 month). We added group ID as a random factor. The minimal model was determined by calculating the change in deviance during stepwise removal of fixed effects. Additionally, Akaike information criterion (AIC) values for each model were considered (Akaike 1974); lower AIC values represent a better fit and corresponded to the minimal model acquired on deviance change grounds. When treatment was found to have a significant overall effect, we conducted 3 planned contrasts for each relevant response variable. First, we compared Herbivore and Own to test for any difference between control treatments. Because these were never found to differ significantly (see Results for details), we tested for an effect of out-group threat (Neighbor and Stranger combined) versus nonthreat conditions (Herbivore and Own combined). Finally, we tested for a difference in response between the 2 out-group threats (Neighbor vs. Stranger).

The aim was to conduct full sets of trials (all 4 treatments) at each group of the 2 data-collection periods. However, 2 groups from the first data-collection period were excluded from the analyses as not all the trials were completed. More than 40% of group members changed between the 2 study periods (separated by 9 months) in 5 of the 6 remaining groups with completed data sets for the first period; group compositions from the middle date in each experimental set were compared. Thus, we treated them as different groups in the analyses; data from only 1 run of the experiment were included from the remaining group to avoid pseudoreplication. Thirteen complete sets of trials were therefore included in the analyses of immediate responses. For the movement data, only the 8 groups from the second field season were available, due to incomplete track data in the first field season.

RESULTS

Immediate behavioral responses

Experimental treatment had a significant effect on the overall response level to the presented feces (Table 1a), time spent at the latrine by group members (Table 1b), and the proportion of the group participating in the latrine activity (Table 1c).

For all 3 response variables, there was no significant difference between the 2 control treatments (Herbivore vs. Own): response level (planned contrast: $Z = 1.54$, $P = 0.326$; effect size ± SE = 2.08 ± 1.35); time spent ($Z = 0.58$, $P = 0.916$; effect size ±

Table 1

Linear mixed models investigating factors affecting (a) response level (raw data), (b) time at latrine (log transformed), and (c) proportion of group participating (square-root transformed) following experimental fecal presentations

	χ^2	df	P		AIC
(a) Response level					
Treatment	**8.82**	**1**	**0.032**		**297.180**
Territory location	0.83	1	0.363		298.353
Pup presence	1.47	1	0.225		297.709
Time of day	<0.001	1	0.980		299.179
		Effect size		SE	
Constant		5.92		1.11	
Group ID		1.75		3.44	
(b) Time					
Treatment	**9.57**	**1**	**0.023**		**55.947**
Territory location	0.11	1	0.737		57.834
Pup presence	0.22	1	0.639		57.728
Time of day	0.52	1	0.471		57.428
		Effect size		SE	
Constant		1.847		0.107	
Group ID		0.104		0.356	
(c) Group proportion					
Treatment	**9.94**	**1**	**0.019**		**−2.752**
Territory location	3.34	1	0.068		−4.088
Pup presence	1.33	1	0.249		−2.081
Time of day	0.08	1	0.783		−0.828
		Effect size		SE	
Constant		0.708		0.066	
Group ID		0.141		0.18	

The analyses used data from 4 experimental trials run in 13 groups. Presented test statistics for the fixed effects were obtained by running the minimal model against the minimal model including the fixed effect of interest. Effect size and SE were extracted from the minimal model: For the constant, they represent the estimated mean value and the variance around this mean; for the random term (Group ID), they represent the variance and the standard deviation. df, degrees of freedom. Significant terms are highlighted in bold.

SE = 0.08 ± 0.14); and proportion of group participating ($Z = 1.04$, $P = 0.654$; effect size ± SE = 0.07 ± 0.07). However, there was a significantly stronger response to out-group threats than to nonthreat treatments. Focal groups exhibited a higher response level ($Z = 2.74$, $P = 0.020$; effect size ± SE = 2.58 ± 0.95; Figure 1a), spent longer at the latrine ($Z = 3.07$, $P = 0.006$; effect size ± SE = 0.30 ± 0.10; Figure 1b), and had more members participating in the latrine activity ($Z = 3.17$, $P = 0.005$; effect size ± SE = 0.16 ± 0.05; Figure 1c) when presented with out-group feces compared with control feces.

Responses did not differ significantly depending on the identity of the out-group threat. There was no significant difference in response level (planned contrast: $Z = 0.46$, $P = 0.956$; effect size ± SE = 0.62 ± 1.35), time spent at the latrine ($Z = 1.05$, $P = 0.650$; effect size ± SE = 0.15 ± 0.15), or proportion of the group participating in the latrine activity ($Z = 0.41$, $P = 0.968$; effect size ± SE = 0.03 ± 0.07) when groups were presented with Neighbor versus Stranger feces.

Movement responses

After controlling for a significant positive influence of pup presence, experimental treatment had a significant effect on the travel speed of groups (Table 2a) and the distance traveled by the group (Table 2b) in the aftermath of fecal presentations. Treatment did not have a significant effect on the direct distance traveled (Table 2c), travel circuity (Table 2d), or the area covered (Table 2e) in the hour after interaction with the feces.

There was no significant difference between the 2 control treatments (Herbivore vs. Own) in either travel speed (planned contrast: $Z = 1.57$, $P = 0.306$; effect size ± SE = 0.12 ± 0.08) or distance traveled ($Z = 1.39$, $P = 0.418$; effect size ± SE = 2.79 ± 2.01). However, there was a significantly stronger response to out-group threats than to nonthreat treatments. Focal groups traveled slower ($Z = 3.59$, $P = 0.001$; effect size ± SE = 0.19 ± 0.05; Figure 2a) and covered less distance ($Z = 3.20$, $P = 0.004$; effect size ± SE = 4.63 ± 1.45; Figure 2b) following interactions with out-group feces compared with control feces.

Responses did not differ significantly depending on the identity of the out-group threat. There was no significant difference in travel speed (planned contrast: $Z = 0.76$, $P = 0.833$; effect size ± SE = 0.06 ± 0.08) or in distance covered ($Z = 0.89$, $P = 0.755$; effect size ± SE = 1.85 ± 2.09) by groups following presentations of Neighbor and Stranger feces.

DISCUSSION

Threatening versus nonthreatening context

Our results show that, as predicted, dwarf mongooses respond strongly to feces from rival groups both in terms of immediate behavioral interactions at the latrine and in subsequent movement patterns. The larger proportion of the group participating in response to feces indicating a territorial threat compared with control conditions corresponds to findings in banded mongooses and meerkats, where individuals encountering latrines containing recent evidence of out-group activity vocalize to recruit other group members (Müller and Manser 2007; Mares et al. 2011). Because relative group size influences contest outcomes in many group-living species, with larger groups tending to win (McComb et al. 1994; Cant et al. 2002; Radford and du Plessis 2004), increased participation from group members in latrine activity may be an attempt to
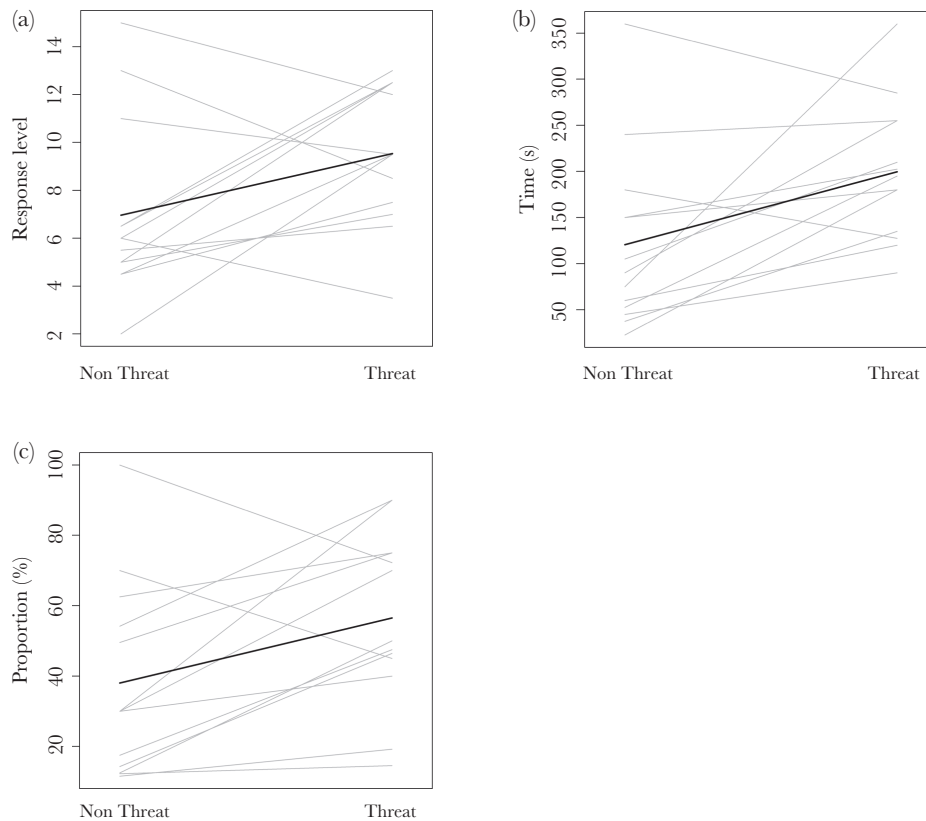
Figure 1
Response of dwarf mongoose groups to experimental presentations of threatening (Neighbor, Stranger) and nonthreatening (Own, Herbivore) feces. Shown are (a) response level, (b) total time spent at the latrine, and (c) proportion of the group participating for each group ($n = 13$) separately (gray lines) and the mean response (black line).

signal resource-holding potential to the intruding group were they to return to that latrine. The increase in time investment during latrine activity in threatening contexts may indicate a larger interest in the presented scent (Müller and Manser 2007; Mares et al. 2011; Sharpe 2015) or a longer time spent by individuals in depositing their own scent. Either way, it is time invested in territorial defense, which is not invested elsewhere (Nolet and Rosell 1994).

Our finding of a stronger immediate response to out-group feces compared with own-group feces contrasts recent work by Sharpe (2015), who found no significant difference in the time individual dwarf mongooses spent inspecting individual fecal samples from different groups (Sharpe 2015). However, our experiment differed from that previous study in a number of potentially crucial aspects. First, we considered group-level responses, whereas Sharpe (2015) investigated the behavior of a single mongoose. Group members are likely to vary in how threatened they are by out-group individuals and some may not respond particularly strongly to them (Desjardins et al. 2008; Mares et al. 2011; Bruintjes et al. 2016). Second, we presented feces from multiple individuals from a group, rather than feces from a single individual. Intruding groups and individuals pose potentially very different threats: Rival groups may be looking to annexe territorial space (Wilson and Wrangham 2003; Kitchen and Beehner 2007; Golabek et al. 2012), whereas individuals may be seeking reproductive opportunities or dominance positions (Mares et al. 2011; Bruintjes et al. 2016). Finally, whereas Sharpe (2015) presented all fecal treatments simultaneously at the same latrine, we presented our treatments at separate times at different latrines because it is unlikely that all would be

naturally encountered together. The stronger response to out-group feces compared with control feces in our experiment suggests that scents of rival groups are threatening and that dwarf mongoose feces do provide some information about group identity.

The slower movement of dwarf mongoose groups, and the shorter distance they covered, after encountering evidence of a territorial threat (feces from rival groups) is in line with findings in solitary southern hairy-nosed wombats *Lasiorhinus latifrons* (Descovich et al. 2012). After encountering fecal samples from conspecific males, individual male wombats moved less as a consequence of increases in vigilance and hiding behavior (Descovich et al. 2012). Male red foxes *Vulpes vulpes* did not decrease their speed, nor did they travel a shorter distance after artificial urine scent-marks were placed within their territory, but a significantly higher proportion of time was spent patrolling the scent-marked area, suggesting a motivation to reclaim that part of the territory (Arnold et al. 2011). Although we did not record the specific behavior of dwarf mongooses in the hour after fecal presentations, it is plausible that slower-moving groups may be more vigilant. This has been shown in the context of predator detection, where slower movement, with intermittent pausing, increases the likelihood of detecting danger (McAdam and Kramer 1998). The dwarf mongooses might therefore have moved slower in an attempt to detect intruders in the vicinity of the latrine, resulting in a shorter distance traveled. Moreover, although no significant difference was found between direct distances from the latrine to the end point an hour later, slower movement may result in more time being spent in the intruded area, asserting the presence of the group as part of

Table 2

Linear mixed models on factors affecting (a) speed of travel (log transformed), (b) distance traveled (square-root transformed), (c) direct distance traveled (square-root transformed), (d) travel circuity (log transformed), and (e) area covered (log transformed)

	χ^2	df	*P*	AIC
(a) Speed				
Treatment	**12.78**	**1**	**0.005**	**−16.205**
Location	0.05	1	0.829	−14.252
Pups	**8.21**	**1**	**0.004**	**−16.205**
Time of day	0.48	1	0.491	−14.680
		Effect size		SE
Constant		−0.649		0.062
Group ID		<0.001		0.151
(b) Distance				
Treatment	**10.68**	**1**	**0.014**	**193.982**
Location	0.47	1	0.492	195.510
Pups	**8.56**	**1**	**0.003**	**193.982**
Time of day	0.75	1	0.387	195.233
		Effect size		SE
Constant		13.658		1.657
Group ID		<0.001		4.028
(c) Direct distance				
Treatment	5.35	1	0.148	175.382
Location	1.80	1	0.180	174.936
Pups	0.25	1	0.617	176.483
Time of day	<0.001	1	0.980	176.733
		Effect size		SE
Constant		6.302		0.646
Group ID		0.703		3.309
(d) Circuity index				
Treatment	4.88	1	0.181	60.320
Location	2.64	1	0.104	58.562
Pups	0.01	1	0.909	61.188
Time of day	0.14	1	0.708	61.061
		Effect size		SE
Constant		0.979		0.09979208
Group ID		<0.001		0.556
(e) Area covered				
Treatment	3.76	1	0.288	80.764
Location	0.44	1	0.509	80.090
Pups	0.14	1	0.705	80.382
Time of day	0.07	1	0.795	80.458
		Effect size		SE
Constant		2.319		0.187
Group ID		0.397		0.674

The analysis used data from 4 experimental trials run on 8 groups. Presented test statistics for the fixed effects were obtained by running the minimal model against the minimal model including the fixed effect of interest. The AIC values for 2 significant fixed effects were extracted from the minimal model including both terms. Effect size and SE were extracted from the minimal model: For the constant, they represent the estimated mean value and the variance around this mean; for the random term (Group ID), they represent the variance and the standard deviation. df, degrees of freedom. Significant terms are highlighted in bold.

a territorial defense strategy. Claiming an area in the aftermath of a contest has been demonstrated in roost selection in green wood-hoopoes, where groups will arrive earlier at the roost after conflict as a means of securing the resource from the neighboring group (Radford and Fawcett 2014).

Neighbor versus stranger context

Our experiment provided no evidence for a difference in response to neighbor and stranger feces in either immediate behavior or in post-latrine movement. One theoretical reason for the similar responses is that NSD is simply not possible from the presented cues. However, previous work on dwarf mongooses has suggested that the deposition of scent-marks by multiple individuals may result in a group signature (Ewer 1968; Rasa 1973), so the relevant information is likely available. Another theoretical reason is that discrimination is possible, but that there has been no selection for a differential response, as has been shown in other contexts and species (e.g., meerkat use of alarm calls; Schibler and Manser 2007). However, NSD appears adaptive in many other species (see Introduction for details), and there are no obvious reasons why dwarf mongooses should be different in this regard. Instead, a lack of apparent NSD may arise for 2 main reasons (see also Frommolt et al. 2003; Battiston et al. 2015).

First, the relative threat posed by neighbors and strangers, rather than being fixed, may fluctuate depending on contextual factors and relative protagonist characteristics. For instance, neighbors may have different resource-holding potential depending on their group size (McComb et al. 1994; Cant et al. 2002; Radford and du Plessis 2004), and previous encounters may determine the nature of the relationship (Müller and Manser 2007; Zenuto 2010; Monclús et al. 2014), with the level of aggression shown by particular neighbors affecting the reaction to them (Hyman and Hughes 2006). Another potential influencing factor is the proportion of borders shared by neighboring groups. In our population, central groups whose territories are surrounded by several others may receive more neighbor pressure than peripheral groups located, for instance, next to the main road. A third possibility might be that the relative threat from neighbors and strangers changes with season; for example, the proximity of neighbors may be viewed as a greater threat when groups have vulnerable young (Temeles 1994; Briefer et al. 2008). In dwarf mongooses, a general increase in scent-marking occurs days prior to the birth of a litter and during the babysitting period (Rasa 1973). Having dependent pups, when intrusions by neighbors can lead to infanticide, could conceivably result in nasty-neighbor relationships during the breeding season, but a dear-enemy effect at other times of the year. These possible drivers of identity-dependent responses to out-groups remain to be explored.

A second general explanation for the lack of a difference in response to neighbor and stranger feces is that responses to intruder scent may be dependent on the identity of the particular individuals who deposit and receive the signal. We considered responses from a group-defense perspective, but that entails the actions of multiple individuals who do not all have the same interests and motivations (Olson 1971; Radford 2004; Crofoot et al. 2008; Crofoot and Gilby 2012). For instance, a link exists between scent-marking and status, with dominant males in particular often contributing more than other group members either because they have a higher interest in territory defense and/or mate-guarding than subordinates (Johnson 1973) or because their better body condition allows greater investment (Gosling and Roberts 2001). Sex of the intruder may also affect the response depending on the sex of the receiver, particularly during the mating season (Roper et al. 1986; Mares et al. 2011) as males and females may be signaling different messages (Wronski et al. 2013). Despite reproductive skew in dwarf mongooses, all group members participate in territorial scent-marking and, unlike other species, both sexes perform handstands (Sharpe et al. 2012). However, it is conceivable that some experimental trials involved higher attendance of, for instance, dominant males, producing overall higher response levels than those that did not, potentially masking NSD.
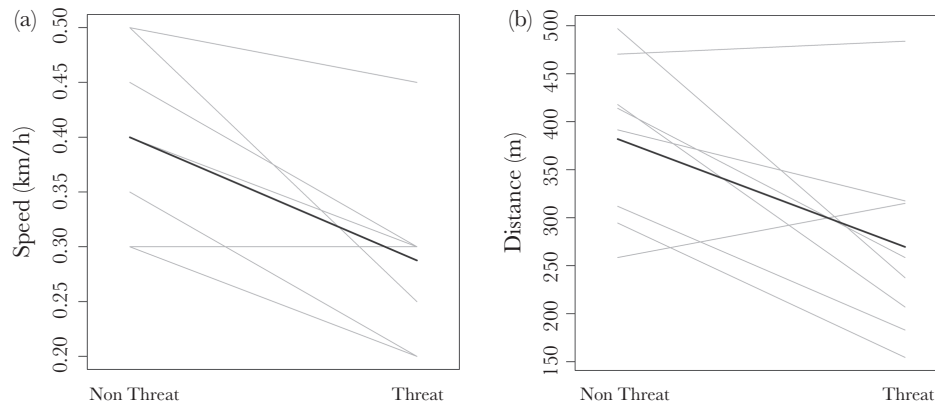
Figure 2

Movement responses of dwarf mongoose groups in the hour after experimental presentations of threatening (Neighbor, Stranger) and nonthreatening (Own, Herbivore) feces. Shown are (a) speed of travel and (b) distance traveled for each group ($n = 8$) separately (gray lines) and the mean movement response (black line).

CONCLUSIONS

Although previous studies have demonstrated an immediate response of territorial groups to the presence of out-group feces, our work demonstrates that there can be longer-lasting effects in terms of movement patterns. This could have energetic costs or consequences in terms of foraging success, predation risk, selection of sleeping burrows, and territory maintenance; these are possibilities, with potential fitness implications, that require consideration in future studies. Our work also suggests that a view of species as exhibiting either a dear-enemy effect or a nasty-neighbor effect may be too simplistic. Further work is needed on social species in terms of both individual contributions to territorial responses to intruders and the fluctuating nature of relationships between resident groups and neighbors or strangers.

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