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

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Running headline: Territorial responses to rival group scents

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

51

52

53 **Keywords: group identity; identity cues; latrine behaviour; out-group conflict; social**  
54 **behaviour; territory defence**

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## 62 **1. Introduction**

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

73

74 The “dear enemy phenomenon” (Fisher 1954), where residents show less aggressive  
75 responses to intruding neighbours compared to strangers, is found in some group-living  
76 species such as green woodhoopoes *Phoeniculus purpureus* (Radford 2005). In general,  
77 neighbours might be less threatening than strangers either because they are known to be  
78 continuously present at a mutual border, whereas intrusions by strangers are spatially and  
79 temporally unpredictable (Jordan et al. 2007), or because they already own a territory,  
80 whereas transient strangers may be looking to usurp residents and take over (Wilson 1980).

81 The “nasty-neighbour phenomenon” (Müller and Manser 2007), where intrusions by  
82 neighbours are countered with higher levels of aggression than those by strangers, is found in  
83 other group-living species such as banded mongooses *Mungos mungo*, where emigration  
84 from the natal territory is undertaken in small groups (Müller and Manser 2007). Small  
85 stranger groups pose less threat to established residents than large neighbouring groups both  
86 in terms of size and intention: stranger groups might simply be passing through, while  
87 neighbours could be seeking to expand their territory (Mech and Boitani 2003; Müller and  
88 Manser 2007).

89

90 Neighbour–Stranger discrimination (NSD) has been shown to be possible through vocal,  
91 visual and olfactory cues. Resident green woodhoopoes responded significantly more rapidly  
92 to playbacks of strangers (posing the threat of permanent territorial eviction) than of  
93 neighbours (causing temporary displacements) (Radford 2005), while other species even  
94 discriminate between different neighbouring groups on the basis of their vocalisations (e.g.

95   vervet monkeys *Cercopithecus aethiops*, Cheney and Seyfarth 1980; chimpanzees *Pan*  
96 *trogodytes*, Crockford et al. 2004). In Jacky dragons *Amphibolurus muricatus*, static  
97 presentations of unfamiliar individuals elicited significantly higher levels of arousal and signs  
98 of information gathering than familiar individuals, supporting dear-enemy predictions (Husak  
99 2004; Van Dyk and Evans 2007). Eurasian beavers *Castor fiber*, European badgers *Meles*  
100 *meles* and African wild dogs *Lycaon pictus* all responded more intensely to scent-marks from  
101 strangers than to those from neighbours (Rosell 2001; Palphramand and White 2007; Parker  
102 2010), while banded mongooses responded more strongly when encountering the scent of a  
103 neighbour than of a stranger group (Müller and Manser 2007).

104

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

123

124   In this study, we use dwarf mongooses *Helogale parvula* to investigate immediate and longer  
125 term responses to simulated territorial intrusions (faeces placed within the focal territory) by  
126 rival conspecific groups. Dwarf mongooses live in cooperatively breeding groups with a  
127 dominant breeding pair; group members sleep, forage and travel together within a shared  
128 territory (Rood 1983; Kern and Radford 2013). Cooperative territorial behaviour involves

129 scent-marking at communal latrines and physical defence when other groups are encountered  
130 (Rasa 1973). Four olfactory channels are used: urine, faecal matter and both cheek-gland and  
131 anal-gland secretions (Rasa 1973). In a captive setting, the introduction of faecal matter from  
132 an unfamiliar pair resulted in increased anal-gland marking by a focal pair compared to when  
133 their own faecal matter was present (Rasa 1973). Recent findings in the field suggest that no  
134 discrimination is made between stranger and own faecal matter when single faeces are  
135 presented alongside one another (Sharpe 2015). However, latrines in the wild are usually  
136 frequented as a group and scent-marks are deposited by multiple group members at such sites  
137 (Sharpe et al. 2012), likely resulting in a group signature (Ewer 1968; Rasa 1973). We  
138 therefore investigated group-level responses to out-group threats as indicated by faeces from  
139 several individuals.

140

141 Our faecal-presentation experiment, considering both immediate behavioural interactions  
142 with the presented faeces and subsequent movement patterns by the territory-holding group,  
143 aimed to answer two main questions. First, do territory holders respond more strongly to  
144 faeces from other groups (out-group threat) than to control faeces (those from their own  
145 group and from herbivores)? Since out-group faeces will be less familiar to individuals than  
146 those from their own group, and out-groups represent a potential threat in terms of resource  
147 loss and territory usurpation, we predicted a stronger response to faeces from rival groups  
148 compared to control faeces. Second, do territory holders respond differentially to faeces from  
149 neighbours and strangers? Neighbouring dwarf mongoose groups commonly contest the  
150 temporary rights to sleeping burrows on the mutual boundary of their territory, while conflict  
151 with transient groups rarely involves sleeping-site contestation and are generally less intense  
152 (Rasa 1987). The majority of observed intergroup interactions take place between  
153 neighbouring groups (unpublished data) and repeated intrusions intensify responses to rivals  
154 in other species (Monclús et al. 2014). We therefore predicted a stronger response to faeces  
155 from neighbours than to those from strangers.

156

## 157 **2. Material and methods**

### 158 **(a) Study site and population**

159 The study was conducted on Sorabi Rock Lodge, a 4 km<sup>2</sup> private reserve in the Limpopo  
160 Province, South Africa (24° 11'S, 30° 46'E), part of southern Africa's Savannah Biome (see  
161 Kern and Radford 2013 for full details). We collected data over two periods: November 2013

162 to January 2014 (summer) and June 2014 to October 2014 (winter). All procedures were  
163 approved by the Department of Environmental Affairs and Tourism, Limpopo Province  
164 (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol  
165 (University Investigator Number: UB11/038).

166

167 The long-term study population consists of eight groups of dwarf mongooses (group sizes  
168 ranging from 3 to 15 individuals), habituated to close human presence on foot and thus  
169 allowing for detailed observation (<5 m) in natural conditions (Kern and Radford 2013,  
170 2014). Individuals can be identified from marks of blond hair-dye (Garnier Nutrisse) applied  
171 using an elongated paint-brush whilst distracting the mongoose with egg. Dominant  
172 individuals are recognised by their higher levels of aggression, feeding displacement and  
173 greeting behaviours (Rasa 1977; Kern et al. 2016). Groups are visited regularly to maintain  
174 habituation, re-apply hair-dye, collect baseline data and keep track of important life-history  
175 events (e.g. pregnancies, births, emigration, dominance changes and deaths).

176

## 177 **(b) Experimental protocol**

178 The experiment aimed to investigate differences in both immediate behavioural responses  
179 and subsequent movement patterns following four different faecal presentations. The four  
180 treatments comprised faeces collected from: a neighbouring group (Neighbour), a non-  
181 neighbouring group (Stranger), the focal group (Own) and a herbivore (Herbivore). Own and  
182 Herbivore represent two forms of control: Own controlled for the presence of conspecific  
183 faecal matter, which might be expected to result in some responses due to intra-group non-  
184 territorial functions (Rasa 1973; Sharpe 2015); and Herbivore controlled for the interference  
185 by the experimenter with the latrine and the addition of faeces. We presented treatments to  
186 the same group on different days in a randomised order; subsequent analysis confirmed that  
187 there was no unintentional bias in the ordering of different treatments (Friedman test:  
188  $\chi^2=2.35$ ,  $n=13$ ,  $p=0.502$ ).

189

190 To standardise between the different mongoose faecal treatments (Own, Neighbour,  
191 Stranger), each presented sample consisted of one faeces from each of four separate group  
192 members, including at least one of the dominant pair. For the Herbivore treatment, we used  
193 four faecal pellets from greater kudu *Tragelaphus strepsiceros* or giraffe *Giraffa*  
194 *camelopardalis* (diameter ~2 cm; same size as dwarf mongoose faeces). Faeces were

195 collected within 5 min of deposition, placed in airtight, sealed plastic bags inside glass pots  
196 while in the field, and stored overnight in a fridge (5°C). Faeces were always used in an  
197 experimental presentation within 1 day of collection (mean±SE=13.0±1.6 h), and there was  
198 no significant difference between treatments in time between collection and use (Friedman  
199 test:  $\chi^2=1.92$ , n=13, p=0.584).

200

201 We conducted faecal presentations at mongoose latrines, which are communal, frequently  
202 used elimination sites. Latrines are recognisable by the accumulation of faecal matter (Rasa  
203 1973) and their location was marked using handheld GPS devices (Garmin Etrex H GPS;  
204 Garmin Europe Ltd., Southampton, Hampshire, UK) during observational data-collection  
205 sessions. After the focal group left their sleeping burrow, the observer tracked the presence of  
206 nearby latrines using the GPS map while following the foraging group. If the group was  
207 approaching a latrine (within 15 m), the observer moved ahead quietly and placed the faecal  
208 presentation on the ground at that site, before moving 5 m away; this distance allowed  
209 detailed observations without affecting latrine activity by the mongooses. We did not conduct  
210 faecal presentations if there had been an inter-group interaction earlier in the day; at least 30  
211 min were allowed to elapse since any other latrine activity before faeces were presented in an  
212 experimental trial.

213

### 214 **(c) Data collection**

215 We defined the start of the focal-group response as the first interaction (sniffing) with the  
216 faecal presentation by any group member. Thereafter, we recorded the following data:  
217 number and identity of individuals present at the latrine (every 30 s); the total time spent at  
218 the latrine by all responders; and the latrine behaviours exhibited (sniffing, urinating,  
219 defecating, cheek-gland marking and anal-gland marking by hand-standing) by all  
220 responders. Cheek-gland marking involves rubbing the corners of both cheeks alternately  
221 against a surface, is predominantly performed by dominant individuals, and is considered a  
222 display of aggression. Anal-gland marking is performed by everting the anal gland pouch  
223 containing anogenital secretions; adopting a “handstand” position, balancing on the forelegs  
224 and swinging the back legs up to mark sloping surfaces, allows individuals to deposit the  
225 scent at an elevated level (Rasa 1973; Estes 1999). We gave each latrine behaviour in the 15  
226 min following the first interaction with the faecal presentation a score, based on its rank  
227 inferred from assumed energy-investment and importance in territorial defence; anal-gland



228 marking by hand-standing is considered the most energetically costly scent-marking  
229 behaviour (Sharpe et al. 2012): sniffing=1, urinating=2, defecating=3, cheek-gland  
230 marking=4, anal-gland marking=5. We summed scores to generate a “response level” value  
231 for the group.

232

233 We collected continuous movement data (track position recorded every 10 s) using a GPS for  
234 the hour after the interaction with the faecal presentation. We imported data via Basecamp  
235 (software version 4.4.6, Garmin Ltd.) into Mapsource (software version 6.16.3, Garmin Ltd)  
236 and stored them as daily movement maps. From these maps, the distance travelled, time of  
237 travel, average speed and the area covered by the track were calculated automatically. To  
238 infer “directness” of travel, we calculated circuitry indexes by dividing the track distance by  
239 the direct distance between the location of the faecal presentation and the location of the  
240 group one hour after the first interaction (Janson 1998; Porter and Garber 2013).

241

#### 242 **(d) Assignment of latrine locations**

243 While the initial aim was to conduct all faecal presentations in the periphery of the territory—  
244 territory location is known to influence the response to intruders in other group-living species  
245 (Furrer et al. 2011; Brown 2013)—this was precluded by the limited range used by our study  
246 population during the data-collection period in the second field season. To classify each  
247 experimental latrine site as either core or periphery, we calculated home ranges using the  
248 movement data collected over the six months preceding the relevant experimental field  
249 season. In the two instances where prior movement data did not extend back six months, we  
250 used all available data (three months in both cases). Six months was chosen as a balance  
251 between including sufficient data (mean±SE observation sessions=50.5±3.8; mean±SE  
252 geographical data points=480±60) and delineating a plausible home range, as space use  
253 varies over time (unpub. data). We transferred the geographical waypoint data from the daily  
254 movement maps for each group during each period into Mapsource (as above) and then into  
255 QGIS (version 2.6.1 Brighton, FOSS). Using the Minimum Convex Polygon (MCP)  
256 algorithm from the plugin AniMove (version 6.16.14, Garmin corp), we calculated MCPs  
257 using 100% of the data point fixes to estimate the full home-range (as in Gilchrist and Otali  
258 2002; Mattisson et al. 2013). Subsequently, the central 50% fixes were used to determine  
259 which latrines were classified as core (within MCP 50) and which as peripheral (outside  
260 MCP 50) (as in José and Lovari 1998; Jędrzejewski et al. 2007).

261

262 **(e) Data analysis**

263 We analysed data using R version 3.1.2 (R Development Core Team 2012). We used mixed  
264 models to take account of repeated data from the same group. Linear Mixed Models (LMMs)  
265 were used throughout since datasets, or their log or square-rooted transformations, fit the  
266 assumptions of parametric testing. We added treatment (Neighbour, Stranger, Own,  
267 Herbivore), territorial location (Core, Periphery), pup presence (Yes, No) and time of day  
268 (AM, PM) as fixed effects. Pup presence was defined as the period of time after birth until  
269 the pups are observed to first forage independently (~1 month). We added group ID as a  
270 random factor. The minimal model was determined by calculating the change in deviance  
271 during step-wise removal of fixed effects. Additionally, Akaike Information Criterion (AIC)  
272 values for each model were considered (Akaike 1974); lower AIC values represent a better fit  
273 and corresponded to the minimal model acquired on deviance change grounds. When  
274 treatment was found to have a significant overall effect, we conducted three planned contrasts  
275 for each relevant response variable. First, we compared Herbivore and Own to test for any  
276 difference between control treatments. Since these were never found to differ significantly  
277 (see Results), we tested for an effect of out-group threat (Neighbour and Stranger combined)  
278 versus non-threat conditions (Herbivore and Own combined). Finally, we tested for a  
279 difference in response between the two out-group threats (Neighbour versus Stranger).

280

281 The aim was to conduct full sets of trials (all four treatments) at each group of the two data-  
282 collection periods. However, two groups from the first data-collection period were excluded  
283 from the analyses as not all the trials were completed. More than 40% of group members  
284 changed between the two study periods (separated by 9 months) in five of the six remaining  
285 groups with completed datasets for the first period; group compositions from the middle date  
286 in each experimental set were compared. Thus, we treated them as different groups in the  
287 analyses; data from only one run of the experiment were included from the remaining group  
288 to avoid pseudo-replication. Thirteen complete sets of trials were therefore included in the  
289 analyses of immediate responses. For the movement data, only the eight groups from the  
290 second field season were available, due to incomplete track data in the first field season.

291

## 292 **3. Results**

### 293 **(a) Immediate behavioural responses**

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

297

298 For all three response variables, there was no significant difference between the two control  
299 treatments (Herbivore versus Own): response level (planned contrast:  $Z=1.54$ ,  $p=0.326$ ;  
300 effect size $\pm$ SE= $2.08\pm 1.35$ ); time spent ( $Z=0.58$ ,  $p=0.916$ ; effect size $\pm$ SE= $0.08\pm 0.14$ );  
301 proportion of group participating ( $Z=1.04$ ,  $p=0.654$ ; effect size $\pm$ SE= $0.07\pm 0.07$ ). However,  
302 there was a significantly stronger response to out-group threats than to non-threat treatments.  
303 Focal groups exhibited a higher response level ( $Z=2.74$ ,  $p=0.020$ ; effect size $\pm$ SE= $2.58\pm 0.95$ ;  
304 Figure 1a), spent longer at the latrine ( $Z=3.07$ ,  $p=0.006$ ; effect size $\pm$ SE= $0.30\pm 0.10$ ; Figure  
305 1b) and had more members participating in the latrine activity ( $Z=3.17$ ,  $p=0.005$ ; effect  
306 size $\pm$ SE= $0.16\pm 0.05$ ; Figure 1c) when presented with out-group faeces compared to control  
307 faeces.

308

309 Responses did not differ significantly depending on the identity of the out-group threat. There  
310 was no significant difference in response intensity (planned contrast:  $Z=0.46$ ,  $p=0.956$ ; effect  
311 size $\pm$ SE= $0.62\pm 1.35$ ), time spent at the latrine ( $Z=1.05$ ,  $p=0.650$ ; effect size $\pm$ SE= $0.15\pm 0.15$ )  
312 or proportion of the group participating in the latrine activity ( $Z=0.41$ ,  $p=0.968$ ; effect  
313 size $\pm$ SE= $0.03\pm 0.07$ ) when groups were presented with Neighbour versus Stranger faeces.

314

### 315 **(b) Movement responses**

316 After controlling for a significant positive influence of pup presence, experimental treatment  
317 had a significant effect on the travel speed of groups (Table 2a) and the distance travelled by  
318 the group (Table 2b) in the aftermath of faecal presentations. Treatment did not have a  
319 significant effect on the direct distance travelled (Table 2c), travel circuitry (Table 2d) or the  
320 area covered (Table 2e) in the hour after interaction with the faeces.

321

322 There was no significant difference between the two control treatments (Herbivore versus  
323 Own) in either travel speed (planned contrast:  $Z=1.57$ ,  $p=0.306$ ; effect size $\pm$ SE= $0.12\pm 0.08$ )  
324 or distance travelled ( $Z=1.39$ ,  $p=0.418$ ; effect size $\pm$ SE= $2.79\pm 2.01$ ). However, there was a

325 significantly stronger response to out-group threats than to non-threat treatments. Focal  
326 groups travelled slower ( $Z=3.59$ ,  $p=0.001$ ; effect size $\pm$ SE= $0.19\pm 0.05$ ; Figure 2a) and covered  
327 less distance ( $Z=3.20$ ,  $p=0.004$ ; effect size $\pm$ SE= $4.63\pm 1.45$ ; Figure 2b) following interactions  
328 with out-group faeces compared to control faeces.

329

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

334

## 335 **4. Discussion**

### 336 **(a) Threatening vs. non-threatening context**

337 Our results show that, as predicted, dwarf mongooses respond strongly to faeces from rival  
338 groups both in terms of immediate behavioural interactions at the latrine and in subsequent  
339 movement patterns. The larger proportion of the group participating in response to faeces  
340 indicating a territorial threat compared to control conditions corresponds to findings in  
341 banded mongooses and meerkats, where individuals encountering latrines containing recent  
342 evidence of out-group activity vocalise to recruit other group members (Müller and Manser  
343 2007; Mares et al. 2011). Since relative group size influences contest outcomes in many  
344 group-living species, with larger groups tending to win (McComb et al. 1994; Cant et al.  
345 2002; Radford and du Plessis 2004), increased participation from group members in latrine  
346 activity may be an attempt to signal resource-holding potential to the intruding group were  
347 they to return to that latrine. The increase in time investment during latrine activity in  
348 threatening contexts may indicate a larger interest in the presented scent (Müller and Manser  
349 2007; Mares et al. 2011; Sharpe 2015) or a longer time spent by individuals in depositing  
350 their own scent. Either way, it is time invested in territorial defence, which is not invested  
351 elsewhere (Nolet and Rosell 1994).

352

353 Our finding of a stronger immediate response to out-group faeces compared to own-group  
354 faeces contrasts recent work by Sharpe (2015), who found no significant difference in the  
355 time individual dwarf mongooses spent inspecting individual faecal samples from different  
356 groups (Sharpe 2015). However, our experiment differed from that previous study in a  
357 number of potentially crucial aspects. First, we considered group-level responses, whereas

358 Sharpe (2015) investigated the behaviour of a single mongoose. Group members are likely to  
359 vary in how threatened they are by out-group individuals and some may not respond  
360 particularly strongly to them (Desjardins et al. 2008; Mares et al. 2011; Bruintjes et al. 2016).  
361 Second, we presented faeces from multiple individuals from a group, rather than faeces from  
362 a single individual. Intruding groups and individuals pose potentially very different threats:  
363 rival groups may be looking to annexe territorial space (Wilson and Wrangham 2003;  
364 Kitchen and Beehner 2007; Golabek et al. 2012), whereas individuals may be seeking  
365 reproductive opportunities or dominance positions (Mares et al. 2011; Bruintjes et al. 2016).  
366 Finally, whereas Sharpe (2015) presented all faecal treatments simultaneously at the same  
367 latrine, we presented our treatments at separate times at different latrines since it is unlikely  
368 that all would be naturally encountered together. The stronger response to out-group faeces  
369 compared to control faeces in our experiment suggests that scents of rival groups are  
370 threatening and that dwarf mongoose faeces do provide some information about group  
371 identity.

372

373 The slower movement of dwarf mongoose groups, and the shorter distance they covered,  
374 after encountering evidence of a territorial threat (faeces from rival groups) is in line with  
375 findings in solitary southern hairy-nosed wombats *Lasiorhinus latifrons* (Descovich et al.  
376 2012). After encountering faecal samples from conspecific males, individual male wombats  
377 moved less as a consequence of increases in vigilance and hiding behaviour (Descovich et al.  
378 2012). Male red foxes *Vulpes vulpes* did not decrease their speed, nor did they travel a shorter  
379 distance after artificial urine scent-marks were placed within their territory, but a significantly  
380 higher proportion of time was spent patrolling the scent-marked area, suggesting a motivation  
381 to reclaim that part of the territory (Arnold, Soulsbury and Harris 2011). Although we did not  
382 record the specific behaviour of dwarf mongooses in the hour after faecal presentations, it is  
383 plausible that slower-moving groups may be more vigilant. This has been shown in the  
384 context of predator detection, where slower movement, with intermittent pausing, increases  
385 the likelihood of detecting danger (McAdam and Kramer 1998). The dwarf mongooses might  
386 therefore have moved slower in an attempt to detect intruders in the vicinity of the latrine,  
387 resulting in a shorter distance travelled. Moreover, although no significant difference was  
388 found between direct distances from the latrine to the end point an hour later, slower  
389 movement may result in more time being spent in the intruded area, asserting the presence of  
390 the group as part of a territorial defence strategy. Claiming an area in the aftermath of a  
391 contest has been demonstrated in roost selection in green woodhoopoes, where groups will

392 arrive earlier at the roost after conflict as a means of securing the resource from the  
393 neighbouring group (Radford and Fawcett 2014).

394

### 395 **(b) Neighbour vs. stranger context**

396 Our experiment provided no evidence for a difference in response to neighbour and stranger  
397 faeces in either immediate behaviour or in post-latrine movement. One theoretical reason for  
398 the similar responses is that Neighbour–Stranger discrimination (NSD) is simply not possible  
399 from the presented cues. However, previous work on dwarf mongooses has suggested that the  
400 deposition of scent-marks by multiple individuals may result in a group signature (Ewer  
401 1968; Rasa 1973), so the relevant information is likely available. Another theoretical reason  
402 is that discrimination is possible, but that there has been no selection for a differential  
403 response, as has been shown in other contexts and species (e.g. meerkat use of alarm calls;  
404 Schibler and Manser 2007). However, NSD appears adaptive in many other species (see  
405 Introduction) and there are no obvious reasons why dwarf mongooses should be different in  
406 this regard. Instead, a lack of apparent NSD may arise for two main reasons (see also  
407 Frommolt et al. 2003; Battiston et al. 2015).

408

409 First, the relative threat posed by neighbours and strangers, rather than being fixed, may  
410 fluctuate depending on contextual factors and relative protagonist characteristics. For  
411 instance, neighbours may have different resource-holding potential depending on their group  
412 size (McComb et al. 1994; Cant et al. 2002; Radford and du Plessis 2004), and previous  
413 encounters may determine the nature of the relationship (Müller and Manser 2007; Zenuto  
414 2010; Monclús et al. 2014), with the level of aggression shown by particular neighbours  
415 affecting the reaction to them (Hyman and Hughes 2006). Another potential influencing  
416 factor is the proportion of borders shared by neighbouring groups. In our population, central  
417 groups whose territories are surrounded by several others may receive more neighbour  
418 pressure than peripheral groups located, for instance, next to the main road. A third  
419 possibility might be that the relative threat from neighbours and strangers changes with  
420 season; for example, the proximity of neighbours may be viewed as a greater threat when  
421 groups have vulnerable young (Temeles 1994; Briefer et al. 2008). In dwarf mongooses, a  
422 general increase in scent-marking occurs days prior to the birth of a litter and during the  
423 babysitting period (Rasa 1973). Having dependent pups, when intrusions by neighbours can  
424 lead to infanticide, could conceivably result in nasty-neighbour relations during the breeding

425 season, but a dear-enemy effect at other times of the year. These possible drivers of identity-  
426 dependent responses to out-groups remain to be explored.

427

428 A second general explanation for the lack of a difference in response to neighbour and  
429 stranger faeces is that responses to intruder scent may be dependent on the identity of the  
430 particular individuals who deposit and receive the signal. We considered responses from a  
431 group-defence perspective, but that entails the actions of multiple individuals who do not all  
432 have the same interests and motivations (Olson 1971; Radford 2004; Crofoot et al. 2008;  
433 Crofoot and Gilby 2012). For instance, a link exists between scent-marking and status, with  
434 dominant males in particular often contributing more than other group members either  
435 because they have a higher interest in territory defence and/or mate-guarding than  
436 subordinates (Johnson 1973) or because their better body condition allows greater investment  
437 (Gosling and Roberts 2011). Sex of the intruder may also affect the response depending on  
438 the sex of the receiver, particularly during the mating season (Roper et al. 1986; Mares et al.  
439 2011) as males and females may be signalling different messages (Wronski et al. 2013).  
440 Despite reproductive skew in dwarf mongooses, all group members participate in territorial  
441 scent-marking and, unlike other species, both sexes perform handstands (Sharpe et al. 2012).  
442 However, it is conceivable that some experimental trials involved higher attendance of, for  
443 instance, dominant males, producing overall higher response levels than those that did not,  
444 potentially masking NSD.

445

### 446 **(c) Conclusions**

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

456

457

458 **Data accessibility:** Data will be made available in Dryad if the paper is accepted for  
459 publication.

460

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465

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692 **Figure legends**

693 **Figure 1.** Response of dwarf mongoose groups to experimental presentations of threatening  
694 (Neighbour, Stranger) and non-threatening (Own, Herbivore) faeces. Shown are (a) response  
695 level (b) total time spent at the latrine and (c) proportion of the group participating for each  
696 group (n=13) separately (grey lines) and the mean response (black line).

697

698 **Figure 2.** Movement responses of dwarf mongoose groups in the hour after experimental  
699 presentations of threatening (Neighbour, Stranger) and non-threatening (Own, Herbivore)  
700 faeces. Shown are (a) speed of travel and (b) distance travelled for each group (n=8)  
701 separately (grey lines) and the mean movement response (black line).

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725 **Table 1.** Linear Mixed Models investigating factors affecting (a) response level (raw data),  
 726 (b) time at latrine (log transformed), (c) and proportion of group participating (square root  
 727 transformed) following experimental faecal presentations.

	$\chi^2$	<i>Df</i>	<i>P</i>	<i>AIC</i>
<b>(a) Response level</b>				
<b>Treatment</b>	<b>8.82</b>	<b>1</b>	<b>0.032</b>	<b>297.180</b>
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
		<i>Effect Size</i>		<i>SE</i>
Constant		5.92		1.11
Group ID		1.75		3.44
<b>(b) Time</b>				
<b>Treatment</b>	<b>9.57</b>	<b>1</b>	<b>0.023</b>	<b>55.947</b>
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
		<i>Effect Size</i>		<i>SE</i>
Constant		1.847		0.107
Group ID		0.104		0.356
<b>(c) Group proportion</b>				
<b>Treatment</b>	<b>9.94</b>	<b>1</b>	<b>0.019</b>	<b>-2.752</b>
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
		<i>Effect Size</i>		<i>SE</i>
Constant		0.708		0.066
Group ID		0.141		0.18

731 The analyses used data from four experimental trials run in 13 groups. Presented test statistics  
 732 for the fixed effects were obtained by running the minimal model against the minimal model  
 733 including the fixed effect of interest. Effect Size and Standard Error (SE) were extracted from  
 734 the minimal model: for the Constant, they represent the estimated mean value and the  
 735 variance around this mean; for the random term (Group ID), they represent the variance and  
 736 the standard deviation.

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743 **Table 2.** Linear Mixed Models on factors affecting (a) speed of travel (log transformed), (b)  
 744 distance travelled (square root transformed), (c) direct distance travelled (square root  
 745 transformed); (d) travel circuitry (log transformed) and (e) area covered (log transformed).

	$\chi^2$	<i>Df</i>	<i>P</i>	<i>AIC</i>
<b>(a) Speed</b>				
<b>Treatment</b>	<b>12.78</b>	<b>1</b>	<b>0.005</b>	<b>-16.205</b>
Location	0.05	1	0.829	-14.252
<b>Pups</b>	<b>8.21</b>	<b>1</b>	<b>0.004</b>	<b>-16.205</b>
Time of day	0.48	1	0.491	-14.680
		<i>Effect Size</i>		<i>SE</i>
Constant		-0.649		0.062
Group ID		<0.001		0.151
<b>(b) Distance</b>				
<b>Treatment</b>	<b>10.68</b>	<b>1</b>	<b>0.014</b>	<b>193.982</b>
Location	0.47	1	0.492	195.510
<b>Pups</b>	<b>8.56</b>	<b>1</b>	<b>0.003</b>	<b>193.982</b>
Time of day	0.75	1	0.387	195.233
		<i>Effect Size</i>		<i>SE</i>
Constant		13.658		1.657
Group ID		< 0.001		4.028
<b>(c) Direct distance</b>				
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
		<i>Effect Size</i>		<i>SE</i>
Constant		6.302		0.646
Group ID		0.703		3.309
<b>(d) Circuitry index</b>				
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
		<i>Effect Size</i>		<i>SE</i>
Constant		0.979		0.09979208
Group ID		<0.001		0.556
<b>(e) Area covered</b>				
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
		<i>Effect Size</i>		<i>SE</i>
Constant		2.319		0.187
Group ID		0.397		0.674

748 The analysis used data from four experimental trials run on eight groups. Presented test  
 749 statistics for the fixed effects were obtained by running the minimal model against the

750 minimal model including the fixed effect of interest. The AIC values for two significant fixed  
751 effects were extracted from the minimal model including both terms. Effect Size and  
752 Standard Error (SE) were extracted from the minimal model: for the Constant they represent  
753 the estimated mean value and the variance around this mean; for the random term (Group ID)  
754 they represent the variance and the standard deviation.

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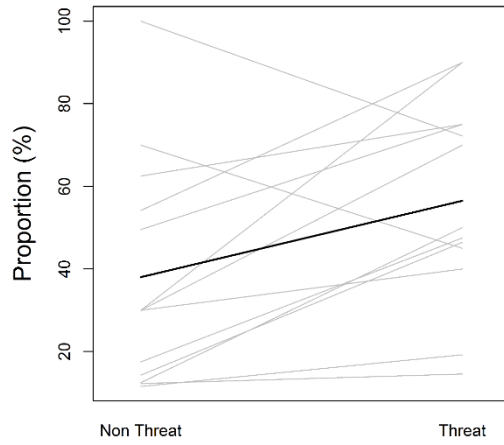
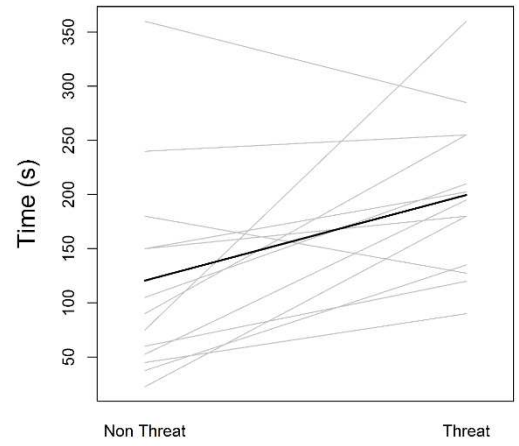
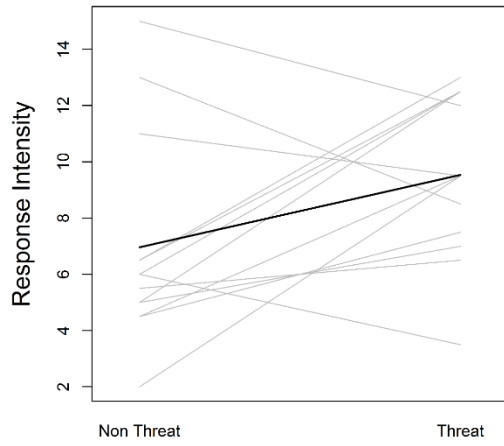
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818 **Figure 2**

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