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Original Article

Location and group size influence decisions in simulated intergroup encounters in banded mongooses

Roman D. Furrer,^a Solomon Kyabulima,^b Erik P. Willems,^c Michael A. Cant,^d and Marta B. Manser^a

^aAnimal Behaviour, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland, ^bBanded Mongoose Research Project, Queen Elizabeth National Park, PO Box 99, Kasese, Uganda, ^cAnthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland, and ^dCentre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Tremough, Penryn TR10 9EZ, Cornwall, UK

In social species that cooperatively defend territories the decision to retreat or attack in contests between groups is likely to depend on ecological and social factors. Previous studies have emphasized the importance of the encounter location or the size of competing groups on the outcome. In addition, the identity of the intruder, whether familiar or stranger, may also play a role. To test whether the same factors affect the resident group's decisions already at the beginning of contests, we simulated intergroup encounters in banded mongooses (*Mungos mungo*). When spotting rival groups banded mongooses emit "screaching calls" which lead group members to bunch up. With playbacks of these calls, we tested how the groups' response was affected by the following factors: 1) the location of the playback in relation to their territory (exclusive use vs. overlap); 2) the number of resident individuals; and 3) the origin of calls (neighbor vs. stranger) used. Subjects were more likely to approach the loudspeakers and arrive within 1 m of the speakers in the exclusive use zone than in the overlap zone. Moreover, larger groups tended to be more likely to move toward the loudspeakers and were also more likely to arrive there. The origin of calls used in the playbacks did not affect the groups' responses. These findings exemplify the importance of the combined effect of location and group size on group decisions during impending intergroup contest. *Key words*: banded mongooses, group decision, group size, intergroup encounter, *Mungos mungo*, territory. [*Behav Ecol* 22:493–500 (2011)]

INTRODUCTION

Contests between territorial groups often include high costs, and it is therefore advantageous for groups to assess the benefits of entering a fight or retreating depending on the ecological and social context (Wilson et al. 2001). In a number of species, fatal consequences of intergroup contests have been described (e.g., various species of ants, Wilson 1971; wolves, Mech 1994; yellow baboons, Shopland 1982; chimpanzees, Goodall 1986; Wilson and Wrangham 2003; Wilson et al. 2004; Townsend et al. 2007; Williams et al. 2008). Due to the severity of such encounters animals should only enter intergroup contests, when the benefits appear to outweigh the costs (Parker 1974). The value of the contested resource may differ for each of the opponents (Austad 1983; Enquist and Leimar 1990). Thus, in situations of impending contest between groups, an efficient assessment of factors influencing the outcome of the contest and consequently an appropriate and coordinated response seem to be crucial for the survival of the group members. If territorial animals can

reliably assess the value of the resource they fight for or the other contestant's fighting ability, it is assumed that they will respond in a context-specific manner (Parker and Rubenstein 1981). Arguments from evolutionary game theory predict that the expected benefits may vary with location relative to the opponents' territorial boundaries and range defense should be highest toward the center of the territory (Maynard Smith 1982). In line with these predictions, resident striped mice (*Rhabdomys pumilio*) are more likely to attack rivals in front of the nest than at territory boundaries (Schradin 2004). And in different species of birds and primates, the responses to calls of extragroup individuals decrease with increasing distance from the center of the defenders' territory (Falls 1982; Raemaekers JJ and Raemaekers PM 1984; Mitani 1985). Furthermore, in contests where groups compete as units, differences in group sizes of the opponents may be a major factor in determining the outcome (McComb 1992; McComb et al. 1994). Research on various species has shown that larger groups tend to defeat smaller ones (e.g., birds: Ligon JD and Ligon SH 1978; ants: Hölldobler 1981; carnivores: Cant et al. 2002; and primates: Cheney 1987). Context-specific assessment may thus be expected during intergroup encounters to adjust the behavior of group members in relation to the relative group size of the opponents (Sekulic 1982; McComb et al. 1994). Recently, automated radio telemetry analyses showed that in intergroup contests of capuchin monkeys (*Cebus capucinus*) the interaction location can outweigh numerical superiority with small resident groups defeating much larger groups near the center of their home

Address Correspondence to R.D. Furrer, Animal Behaviour, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland. E-mail: roman.furrer@zool.uzh.ch.

M.B. Manser is now at Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

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range (Crofoot et al. 2008). Hence, although analyzing contest outcome in social species that show cooperative territorial defense, it is necessary to focus on the interaction between territory location and group size.

Another case of context-specific territorial response is when territory holders differentiate between neighbors and strangers. In flat lizards (*Platysaurus broadleyi*), males respond less aggressively toward neighbors than strangers (Whiting 1999), which is described as the “dear enemy effect” (Fisher 1954; reviewed in Ydenberg et al. 1988; Temeles 1994). Alternatively the opposite phenomenon, called the “nasty neighbor effect” (Müller and Manser 2007), has been described for some species with intense competition between neighbors. Here, individuals respond more intensely to familiar neighbors than to strangers (Godard 1993; Olendorf et al. 2004; Müller and Manser 2007). Thus, social living animals may only attack intruders, which represent a threat to them, because reduced aggression allows conservation of time and energy and reduces the risk of injuries (Wilson 1975).

In this study, we investigated whether the same factors shown to determine the outcome of contests, already influence the group’s decisions at the beginning of simulated intergroup encounters in banded mongooses (*Mungos mungo*). Banded mongooses are territorial cooperative breeders whose home ranges often overlap with those of their neighbors (Rood 1975; Müller and Manser 2007). They mark their home range borders with faeces, urine, and secretions of the anal glands, which are inspected intensively when encountered by neighbors (Rood 1975; Müller and Manser 2007). Competition between social groups is intense, and intergroup encounters are common and may involve withdrawal of one group but often include physical contact and severe aggression and may sometimes have fatal consequences (Rood 1975; Cant et al. 2002; Gilchrist and Oтали 2002; Müller and Manser 2007). During our study period, we witnessed 2 incidents of individuals within the study population being involved in fatal intergroup aggression (Furrer RD and Kybulima S, personal observations). Most encounters take place when social groups come across each other in the overlap zones of their home ranges, but sometimes encounters can take place deep within the home range of a group (Cant et al. 2002). Encounters are initiated when individuals detect rivals, stand erect, and start producing screeching calls (Figure 1), which result in the group members bunching together (Cant et al. 2002; Furrer and Manser 2009). Consequently, individuals of the second group normally also see or hear their rivals and respond with calling and bunching up. In the later stages of the encounter, bunched groups might face each other closely and individuals

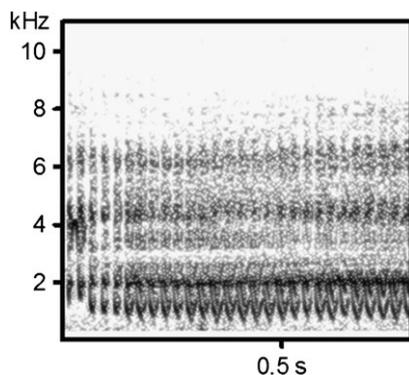


Figure 1
Spectrogram of a screeching call produced at the beginning of an intergroup encounter (fast Fourier transformation length: 1024, Flat Top window, overlap: 96.87%, time resolution 4.25 ms, frequency resolution: 47 Hz).

of both groups may fan out and engage in one-to-one fights or chases until one of the groups retreats (Cant et al. 2002).

We investigated whether social groups respond in a context-specific manner at the beginning of intergroup encounters. With playbacks of screeching calls, we simulated intruding mongooses that had spotted the resident group and started calling. In particular, we investigated how the resident group’s responses were affected by the location of the playback (exclusive use zone vs. overlap zone), by the number of individuals of the resident group that were present and by the origin of the call (neighbor vs. stranger) used in the playbacks. We predicted, according to evolutionary game theory (Parker 1974), that the location of the playback influenced the residents group’s responses. We also predicted that the number of individuals of the resident group would influence their group responses. Banded mongooses can discriminate between olfactory cues of neighbors and strangers (Müller and Manser 2007). However, as screeching calls do not show group-specific features (Furrer and Manser 2009), we predicted that in playbacks the origin of calls used would not have an impact on the group’s responses.

MATERIALS AND METHODS

Study site and animals

This study was conducted between October 2006 and November 2007 on a wild population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (lat 0°12′ S, long 29°54′ E). The vegetation of the study site is mainly short grassland interspersed with numerous dense thickets. Details on habitat and climate are given elsewhere (Cant 2000; De Luca and Ginsberg 2001). The study population consisted of 6 habituated social groups allowing close-range observations and playback experiments. Additionally, we collected data on the spatial distribution of 2 semi-habituated groups and 1 wild group. Group sizes ranged from 7–44 individuals. Animals were classified as adults (>12 months, individuals who have attained reproductive stage or who display secondary sex characteristics which happens at the age of 12 month ca. in banded mongooses) and non-adults (<12 months). For individual identification, which is needed to exactly count the number of adults and non-adults present on a given day, all individuals were trapped on a regular basis. Adults were fitted with color-coded plastic collars. Subadults and infants were marked by shaving a small area of fur of the rump, and pups were individually marked by coloring small areas of fur with hair dye. All individuals were located, trapped, and marked using methods that are in accordance with ASAB/ABS guidelines for the use of animals in research and are described in detail elsewhere (Cant 2000; Hodge 2007; Jordan et al. 2010).

Home range estimation

To assess whether the chosen locations for the playback experiments were within either the exclusive use or overlap zone of each focal group’s territory, home range areas were calculated. To do so, location data were recorded in the field using handheld Garmin 12 GPS units. Coordinates were collected every 15 min after the group had left its overnight den, continuing until the end of the observation period. All GPS data were imported into a Geographic Information Systems model of the study area for further analysis. Potential shifts in home range use over time were accounted for by exclusively considering GPS coordinates collected over the 9-month period immediately preceding the experimental day. Moreover, to minimize serial dependence between GPS points, we

extracted a single randomly selected coordinate from each observation session (Jordan et al. 2007). These were subjected to the kernel density estimation algorithm as implemented in the HRT tools plug-in (Rodgers et al. 2007) for ArcMap 9.0 (Environmental Systems Research Institute, Redlands, CA), using a fixed Gaussian kernel (Worton 1989). Because, in some instances, least squares cross validation failed to minimize, we manually set the kernel's smoothing factor to 0.4 times its reference bandwidth, as this yielded the biologically most informative estimates. Home range areas were subsequently delineated by a 95% volume isopleth. For each experiment, home range areas were calculated for the focal group as well as all neighboring groups, relying on 146 ± 54 (mean \pm standard deviation) coordinates per group (range: 55–249), which is sufficient for home range analysis (Seaman et al. 1999; Börger et al. 2006). Groups were lastly classified as “neighbors” (overlap of the 95% isopleths) or “strangers” (no overlap of the 95% isopleths).

Recording of screeching calls

We recorded calls that were emitted during the first stage of encounters between 2 groups of banded mongooses when members of the 2 different packs saw each other, stood erect and started calling. We quickly moved to the place where the rival banded mongooses were sighted and identified the caller. Calls were recorded within 3 m of the caller using a Marantz PMD670 solid-state recorder (.wav format, sampling frequency of 44.1 kHz, resolution 16 bit) and a Sennheiser ME 66/K6 directional microphone. We recorded calls from several individuals per group during 14 intergroup encounters involving each of the 6 habituated groups.

Playback experiments

Test stimuli

For each playback, we selected screeching calls of a particular foreign group with a good signal to noise ratio. To simulate several intruders, we created 2 different files containing a series of calls that lasted for 30 s using AVISOFT-SASLab pro 4.38. These files were played back from 2 loudspeakers (JBL on Tour; frequency range: 100 Hz–20 kHz, power consumption: 6 W maximum) at the same time. We avoided pseudoreplication by creating 2 unique files for each playback. We standardized the number of calls used for each playback. This was done because firstly the members of the resident group often do not see all intruders as vision can be blocked by vegetation. Secondly, usually not all intruders call at the same time. Therefore, for members of the resident group, it may often be difficult to assess how many intruders are present. The amplitude of the calls used in the playbacks was adjusted to the observed amplitude of calls (max. 80 dB) when subjects encountered foreign mongooses and was measured with a digital sound level meter SL-100 (Voltcraft; sound level range: 30–130 dB, frequency range: 31.5 Hz–8 kHz, response time: 100–125 ms, resolution 0.1 dB).

Experimental design

Playbacks were conducted between May and November 2007. Prior to playback experiments, we followed the focal group of banded mongooses on foot for at least 30 min and recorded the presence of individual group members. We only performed playbacks if the focal group had not encountered rival conspecifics or predators during this period. We then placed the 2 loudspeakers on the ground along the predicted foraging route with a distance of 2 m between them. The loudspeakers were covered by vegetation, and each of them was connected with a Marantz PMD670. We then selected a location in an open area 25 m from the speaker, to gather the

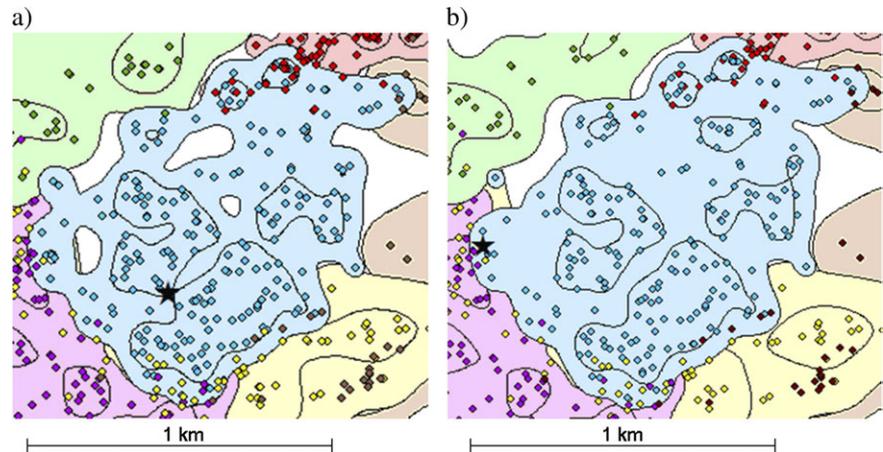
focal group prior to the playback as “start location”. We attracted the individuals to the start location by distributing a small quantity of bait (ca. 20 g of a mix of rice and gravy) on the ground within a circle area of 1 m diameter. As soon as individuals finished searching for bait and began to move away again the playback was started. To collect data on the subjects' responses, one person recorded their behavior at the start location using a camcorder (Sony mini DV Digital Video Camera, model DCR—HC37E), whereas another person watched at a distance of 5 m from the speakers, to make detailed observations of the area close to the speaker. Focal groups always responded by bunching up and then subjects started moving as a close unit. We recorded the following group responses to playbacks: 1) the first movement direction of the focal group as an immediate response; 2) whether they arrived within 1 m of the speakers as a final response; and 3) if the focal group arrived there, we measured the latency to reach the speakers for the first subject using a stopwatch (M-Quartz alarm chronograph, Zurich, Switzerland). By analyzing these 3 types of group responses, we investigated whether the individuals of the resident group 1) confronted the opponents immediately; 2) if they confronted their opponents to defend their territory at all; and 3) on confrontation, how fast they arrived at the loud speakers to confront their simulated opponents. To avoid habituation, only one playback was conducted per group per day followed by a period of at least 7 days without the same or a similar type of playback. We performed the playbacks either in an area of exclusive use of the focal group (exclusive use zone: where we had not recorded foreign mongooses during the 9-month period prior to the experiment; however, foreign mongooses may still occasionally have entered this area; Figure 2a) or in a border area shared with one or several neighboring groups (overlap zone; Figure 2b). We counted the number of group members present during the playbacks (adults, non-adults). This number could vary slightly within the social groups because some individuals may have died or disappeared or juveniles became adults in the time between the playbacks. In each group, we conducted all 4 playback combinations (exclusive use zone-stranger, exclusive use zone-neighbor, overlap zone-stranger, and overlap zone-neighbor) in a randomized order.

Statistical analyzes

Statistical tests were performed using R 2.8.1 (R Development Core Team 2008). To analyze the factors that might affect the group's immediate and final responses to playback of screeching calls, we conducted generalized linear mixed-effect models (see Crawley 2002, Bolker et al. 2009) with binary response variables (for example: focal group arrives within 1 m of the speakers or not), binomial error structure, and logit-link function. We controlled for the repeated sampling of the same group with “group” fitted as a random factor (Crawley 2002) using the package lme4 (Bates et al. 2008). We first constructed full models, including the 3 fixed factors (playback location, number of group members, and calls origin) and tested the overall significance of the full model against the null model including the intercept and the random factor only (Johnson and Omland 2004). Because we observed that adult individuals can be more involved in intergroup interactions than non-adults, we secondly also constructed the same full models but replaced the factor “number of group members” with “number of adult individuals”. We then used the corrected Akaike's Information Criterion (AICc: Hurvich and Tsai 1989) to select the most parsimonious model with the best fit to the data (Johnson and Omland 2004). This approach avoids problems of repeated significance testing (Mundry and Nunn 2009). We conducted likelihood ratio (LR) tests to test the overall

Figure 2

Sample home ranges maps of a focal group (light blue in on-line color version of this figure) and the neighboring social groups are shown. Each home range is confined by the 95% fixed kernel line, and core areas for each home range are confined by the 50% fixed kernel line. Each dot represents a group's location that was randomly selected from all the GPS locations collected during an observation session. GPS points collected during a period of 9 months prior to the playback were incorporated in the maps. The stars represent the locations of playbacks, which were conducted either in an area used exclusively by the focal group (exclusive use zone; figure 2a) or in an area shared with neighboring groups (overlap zone; figure 2b).



significance of each model compared with the null model and the significance of each individual factor compared with a reduced model without the factor of interest. Because the LR tested against a chi-square approximation tend to overestimate effect size (Bolker et al. 2009), we used parametric bootstrapping with 1000 Monte Carlo simulations to generate a distribution of LR from the fitted parameter estimates and tested the observed LR against this distribution (Faraway 2006). For the Monte Carlo simulations, we used the packages *arm* (Gelman et al. 2007) and *faraway* (Faraway 2005).

Furthermore, in playbacks where subjects arrived at the speakers, we analyzed whether the group size of the focal group influenced the time to approach the speakers. After counting the number of individuals present in each playback experiment, we calculated a mean group size and assigned each group a rank according to group size. We conducted Spearman rank correlations to test whether the time to approach the speakers correlated with the groups' ranks and to investigate whether the number of individuals of all age categories, and the number of adult individuals present in each experiment correlated with the time to approach the speakers.

RESULTS

Immediate response to playbacks

Focal groups responded to all playbacks of screeching calls. At first, subjects typically responded by producing worry calls (Supplementary Figure S1; see Müller and Manser 2007) and looking toward the speakers while standing on their hind legs. Then subjects bunched up and often produced screeching calls themselves and sometimes scent marked other mongooses and scent marked the ground. Afterward, all group members either moved toward the speakers or away from them, whereby they often produced moving calls (Supplementary Figure S2). Group members mainly moved as a cohesive group, but sometimes some individuals moved off before others. For the analyses, we used the full model as the exclusion of any of the parameters did not improve the model fit by 2 AICc units. The full model for the immediate response explained significantly more variance in the data than the null model (LR = 18, DEGREES OF FREEDOM [df] = 3, $P = 0.006$). The first movement direction of the subjects was influenced by the location of the playback.

Focal groups were more likely to approach the speakers in the exclusive use zone than in the overlap zone (LR = 11, df = 1, $P = 0.016$; see Table 1a for the values of the predictor variables in the full model). The subjects' first movement direction was also influenced by the number of group members of the resident group. Larger groups tended to be more likely to move toward the speakers than small ones (LR = 7.07, df = 1, $P = 0.073$; Figure 3a). Whether the calls used in the playbacks were recorded from a neighbor or a stranger group did not influence the resident groups' first movement direction (LR = 0.22, df = 1, $P = 0.55$). When we replaced in the full model the number of group members with the number of adult individuals present, the groups with more adult individuals were significantly more likely to move toward the speakers as an immediate response than groups with fewer adult individuals (full model against null model: LR = 21, df = 3, $P = 0.003$; number of adult individuals present: LR = 10, df = 1, $P = 0.024$; Table 1b, Figure 3b). The LR and the P values of the factors playback location and calls origin remained very similar to the ones of the full model including all group members.

Table 1
Factors influencing the focal group's immediate response to simulated intrusion playbacks

Predictor variable		β (estimate) \pm SE	z	P value	
Immediate response					
	Intercept	a	-1.14 \pm 3.88	-0.29	0.77
Playback location		b	0.09 \pm 5	0.018	0.98
	a	4.3 \pm 1.8	2.39	0.017	
Group size	b	4.04 \pm 1.64	2.46	0.014	
	a	-0.28 \pm 0.14	-1.96	0.049	
Call origin	b	-0.5 \pm 0.3	-1.68	0.093	
	a	0.61 \pm 1.78	0.46	0.65	
	b	0.76 \pm 1.66	0.34	0.731	

Shown are the values for all group members (a) and adult individuals only (b) for the predictor variables (playback location; group size; and call origin) used in the generalized linear mixed-effect models, SE, standard error.

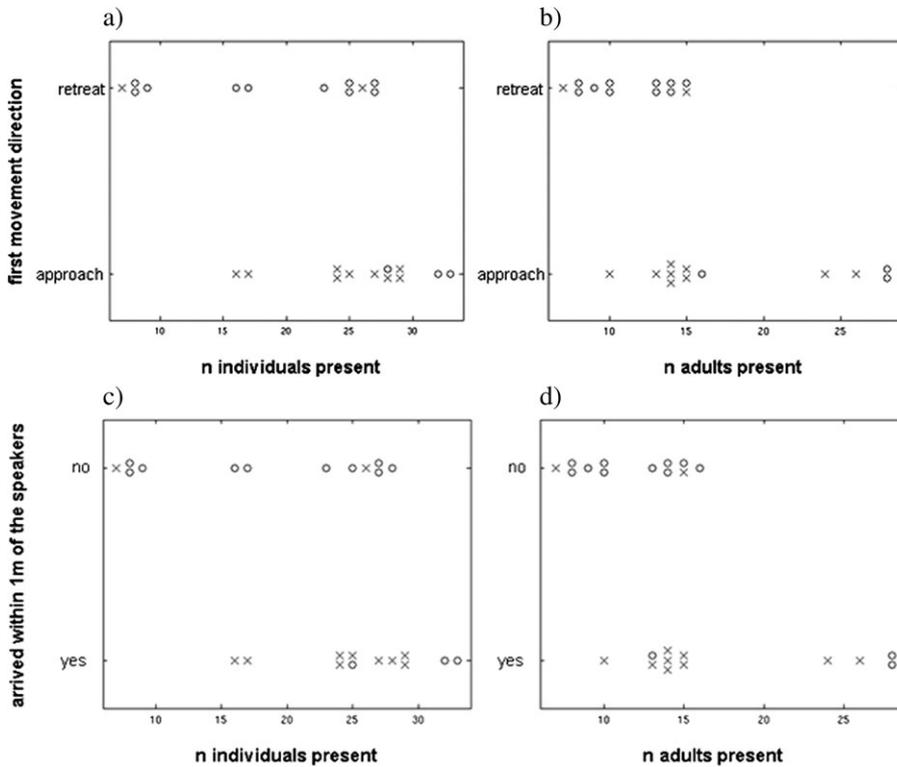


Figure 3
The effect of (a) the total number individuals including non-adults and adults and (b) for the number of adults only (more than 1 year old) present during the playbacks on the likelihood to approach the speakers as an immediate response (a), (b) or to arrive within 1 m of the speakers as a final response (c), (d). (o) represent playbacks conducted in the overlap zone, (x) represent playbacks carried out in the exclusive use zone.

Final response to playbacks

The focal groups’ final responses were influenced by the playback location and group size of the focal groups but not by the origin of the calls. The reduced model with the exclusion of “calls origin” improved the model fit by 2 AICc units and explained for the final response significantly more variance in the data than the null model (LR = 16.1, df = 2, $P = 0.007$). Subjects were more likely to approach to within 1 m of the speakers in the exclusive use zone of their territory than in the overlap zone (LR = 11.4, df = 1, $P = 0.001$; see Table 2a for the values of the factors in the reduced model), and larger groups were more likely to arrive at the speakers than were smaller groups (all groups members: LR = 5.11, df = 1, $P = 0.022$; Figure 3c). When replacing the number of group members with the number of adults present, groups with more adult individuals were also more likely to arrive at the speakers than groups with fewer adults (reduced model against null

model: LR = 17.5, df = 2, $P = 0.001$; number of adult individuals present: LR = 6.5, df = 1, $P = 0.025$; Table 2b; Figure 3d). The LR and the P values of the factors playback location and call origin remained very similar to the ones of the reduced model including all group members.

Time to arrive at the speakers

Group size was negatively correlated with the time to arrive at the speakers, with large groups arriving there faster than small groups (Spearman rank correlation; $r_s = -0.878$, $N = 13$, $P < 0.001$; Figure 4a). The number of individuals of all age categories and the number of adult individuals present during the playbacks were negatively correlated with the time to arrive at the speakers (Spearman rank correlation; all age categories: $r_s = -0.848$, $N = 13$, $P < 0.001$; Figure 4b; adult individuals: $r_s = -0.813$, $N = 13$, $P = 0.001$; Figure 4c).

Table 2
Factors influencing the focal group’s final response to simulated intrusion playbacks

Predictor variable		β (estimate) \pm SE	z	P value
Final response				
	Intercept	a	0.116 \pm 4.670	0.025
	b	-0.140 \pm 4.106	-0.034	0.973
Playback location	a	5.481 \pm 2.176	2.519	0.012
	b	4.532 \pm 1.736	2.610	0.009
Group size	a	-0.377 \pm 0.213	-1.771	0.077
	b	-0.480 \pm 0.297	-1.618	0.106

Shown are the values for all group members (a) and adult individuals only (b) for the predictor variables (playback location; group size; call origin) used in the generalized linear mixed-effect models, SE, standard error.

DISCUSSION

Banded mongoose group decisions to retreat or attack at the beginning of simulated intergroup encounters depended on the experiment location and the number of resident individuals present but not on the origin of calls played back to them. Resident groups reacted in situations of impending contest in a context-specific manner with the location of the playback influencing the first movement direction and the likelihood to arrive at the speakers. Subjects were more willing to move toward and arrive at the speakers in the exclusive use zone of their territory than in an overlap zone used by 2 or more groups. These results are in line with the ultimate explanation derived from evolutionary game theory based on the outcome of contests. Specifically, the decision to participate in intergroup conflicts and the outcome of them can be predicted from the location relative to the opponents’ territorial boundaries and appear to be highest toward the center of the territory (Parker 1974; Maynard Smith 1982).

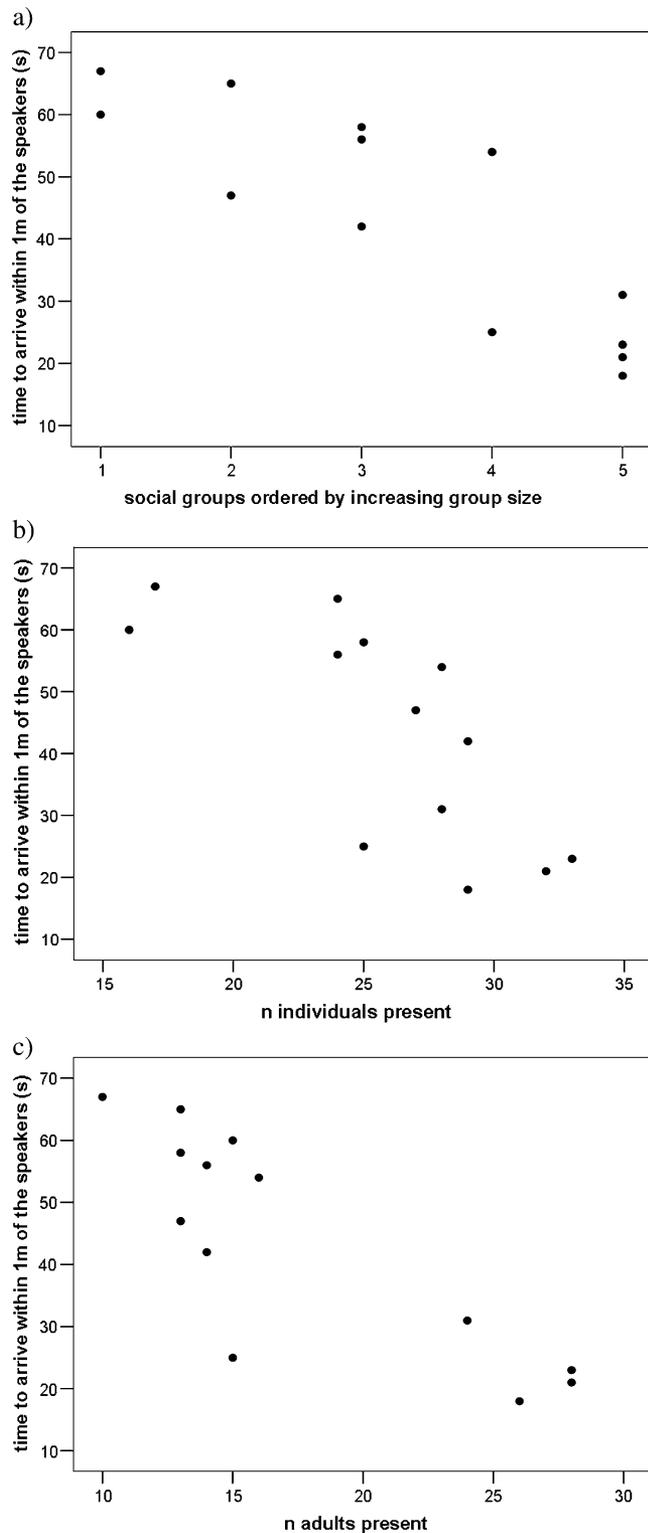


Figure 4
The time to arrive within 1 m of the speakers (s) depending on: (a) social groups ordered by increasing group sizes, (b) the total number of individuals present during the playbacks, and (c) the number of adults present. Note that the smallest study group is not included in the graph as it never arrived within 1 m of the speakers.

As a proximate explanation, the conflict hypothesis (Tinbergen 1952; Hinde 1970) explains the variation in territorial defense of single individuals as a result of the interaction between

aggression and fear, which are opposing motivational states. When aggressive tendencies exceed fearful tendencies, an individual is likely to attack (Archer 1988). This interaction between aggression and fear may equally influence the group's decision in an impending intergroup encounter. Experiments with single individuals showed that male sticklebacks (*Gasterosteus aculeatus*) attack neighbors more intensely inside their territory than outside (Bolyard and Rowland 2000) and striped mice chase away intruders inside their own territory but not at the territory boundaries (Schradin 2004). In group living species, little is known about the influence of encounter location on the group's behavioral responses. In gibbons (*Hylobates lar*), responses to calls of extragroup individuals decrease with increasing distance from the center of the defenders' territory (Raemaekers JJ and Raemaekers PM 1984). Moreover, in capuchin monkeys (*C. capucinus*), small resident groups appear capable of defeating much larger groups near the center of their home range (Crofoot et al. 2008). In banded mongooses, where competition between social groups is intense and intergroup encounters are common, context-specific decisions are essential to avoid unnecessary costs. In areas of overlapping home ranges, the tested groups retreated frequently and thus avoided the potentially severe consequences of a contest. In the exclusive use zone of their territory, however, groups almost always advanced and arrived at the location of the loudspeakers. Thus, it seems that for banded mongooses the value of the resource (Parker 1974, Maynard Smith 1982) "exclusive use zone," where the resident group has more or less exclusive access to its resources, is higher than the value of overlapping areas.

The direction of first movement in response to playbacks tended to be influenced by the total number of individuals of the resident group, whereas this immediate response was significantly influenced by the number of adult individuals present. Both the total number of group members and the number of adult individuals had an effect on the likelihood to arrive at the speakers. The resident group's decisions were therefore influenced by the number of defenders, with larger groups being more likely to approach and to risk a contest. Wilson et al. (2001) suggested that numerical assessment is widespread among species with intergroup contest. Assessment of the opponent's strength in numbers was experimentally shown in lions (*Panthera leo*), where females are more willing to enter contests in which their side has a numerical advantage. For example, they were more likely to approach a single roar than a chorus of 3 strangers' roars (McComb et al. 1994). Assessment of the number of intruders was also shown in green woodhoopoes (*Phoeniculus purpureus*), where members of the resident group vocalized longer in response to intrusions by larger groups (Radford 2003). As all group members cackle loudly during their vocal rallies, vocalizations allow an accurate assessment of the opponent's strength. In banded mongooses, however, not all intruders call at the same time after having spotted the rivals. Hence, numerical assessment of the intruder's group size at the beginning of an intergroup encounter seems unlikely.

Empirical studies have shown that the fighting behavior is influenced by experience of previous fights and not only on relative assessment of the opponents' strength. When some fish lose a fight they tend to lose again (Chase et al. 1994; Hsu and Wolf 1999), and in threespine sticklebacks (*G. aculeatus*), territorial aggression is modified by the individual's past fighting experience (Bolyard and Rowland 2000). In our study, independent of the playback location, the smallest group always retreated, whereas the largest group always advanced. As fights between groups of banded mongooses are usually decided by group size with larger groups defeating smaller ones (Cant et al. 2002), it seems likely that the group's

decisions at the beginning of an intergroup encounter is influenced by experience of previous fights and not only on relative assessment of the opponents' strength. The willingness of the largest group to approach the speakers and arrive there to risk a contest may also be due to their better body condition compared with the 5 other tested groups. This group had access to garbage dumps in their territory, and adults of this refuse-feeding group were heavier than non-refuse-feeding adults (Otalí and Gilchrist 2004; Furrer RD and Kybulima S, personal observation). Numerical advantage and their higher body mass may have contributed to them winning most contests. Thus, it suggests that experiences of previous encounters may have influenced their decisions to always approach and arrive at the speakers. Larger groups also arrived faster to face the simulated intruders, indicating that they also seem to be ready to confront their rivals more quickly.

The call origin did not have an effect on the focal group's immediate and final responses.

Whether the calls used in the playbacks were recorded from individuals of a neighbor or a stranger group did not influence the focal group's first movement direction and the likelihood to arrive at the speakers. In some species, territory holders differentiate between familiar neighbors and strangers (Temeles 1994; Radford 2005). Banded mongooses discriminate between the scent marks of neighbors and strangers (Müller and Manser 2007). This ability seems to be adaptive because neighbors pose a considerable threat as potential usurpers of territories and competitors of mates (Cant et al. 2002), whereas, in contrast, strangers commonly represent small, single-sex dispersing splinters that are typically outnumbered by their same-sex individuals of the resident group and thus pose little threat (Cant et al. 2001; Müller and Manser 2007). However, in contrast to their response to olfactory cues, focal groups did not respond differently to the screeching calls of neighbors versus the screeching calls of strangers. As screeching calls do not show group-specific features (Furrer and Manser 2009), it seems likely that banded mongooses cannot recognize calls of particular rival groups. Furthermore, because typically home ranges of more than 2 neighboring groups overlap, it seems likely that members of the resident group do often not know which opponent they face at the beginning of an intergroup encounter. Thus, resident groups do not seem to gather information about the identity of the intruders using acoustic cues. Instead, the location and the number of defenders seem to have more influence on the group's decisions at the beginning of an intergroup encounter.

The combination of encounter location and the group size of the resident group influence the decisions to retreat or to approach and attack the intruders in banded mongoose. These results are in line with predictions of evolutionary game theory suggesting that the expected benefits may vary with the location relative to the opponents' territorial boundaries. Our results suggest that in banded mongooses decisions in impending contests are made context specifically and that experience of previous encounters, as shown for solitary living species, might play an important role in the decision-making process. We conclude that the same factors that affect the outcome of contests already influence the group decision to retreat or attack from the very beginning of an encounter. As such, our findings likely represent a general pattern used by social species that show cooperative territorial defense. It appears that the decision to participate and the outcome of such contests are highly predictable from a few factors: the location of the encounter, group size.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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