Title

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Abstract

Evolutionary game theory posits that competitive ability affects the initiation of conflicts. When contests occur among groups, competitive ability is generally measured as the size of the group and larger groups are expected to win against smaller groups. However, in some cases, individual participation during intergroup conflicts appears unaffected by competitive ability. To test whether these instances might be due to an unduly strict definition of participation, I re-evaluate the responses of gray-cheeked mangabeys (*Lophocebus albigena*) to the calls of real and simulated neighboring groups. In contrast with previous analyses, I consider multiple measures of group size, treat movement responses as a continuous variable, and evaluate individual responses ($N = 201$ focal follows). Males made stronger approaches toward calling neighbors than females, though both sexes tended to retreat from groups that were <500 m away and to approach more distant neighbors. Individuals in small groups retreated while those in large groups both approached and retreated. There was no evidence of a collective action problem: in fact, approaches were more likely within large groups than small groups, and approaches were stronger when at least one other individual within the focal group made a dramatic approach toward the caller. The absence of a group size effect is attributable to coarse methods in some contexts and to a stronger effect of collective behavior or resource-related motivation in other contexts.

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Introduction

Aggression is a widespread and common feature of animal sociality and though claws, teeth, and horns are often involved, relatively few incidents result in wounding or death (Maynard Smith and Price 1973). Evolutionary game theory of animal contests resolves this apparent contradiction by predicting that weaker or less motivated animals should back down, rather than escalate, in the face of stronger or more motivated opponents, and that the latter should approach (offensive aggression) or hold their ground (defensive guarding of a resource or area; Maynard Smith and Parker 1976; Maynard Smith and Price 1973; Parker 1974). Moreover, where information about relative competitive ability is subtle or absent, contests escalate as a means of testing the other party and gauging relative ability until the likely winner becomes clear. In group-level conflicts, a typical measure of competitive ability is group size: i.e., the number of individuals overall, of the age or sex class that tends to participate in such interactions, or the number of active participants in the contest (Brown and Crofoot 2013). In some cases, group size is weighted by the summed strength or skill of each group member or participant (Batchelor *et al.* 2012), though this approach is rarely feasible for wild primate populations (*cf.* Harris 2010).

Group-wide performance depends upon the actions of its constituents, and whether an individual actively participates, maintains a passive presence, or flees from the contest may affect the success of the group as a whole. Individual behavior, in turn, is largely determined by whether the benefits of participation (or defection) outweigh the expected costs, and this ratio typically varies with rank, age, sex, and other characteristics (Kitchen and Beehner 2007; Langergraber *et al.* 2017; Watts and Mitani 2001). Controlling for these idiosyncrasies, the evolutionary game theoretic prediction that smaller groups will back down from larger groups should translate into a decreased likelihood of participation for individuals when the numeric odds are against them, i.e., when their group is substantially smaller than the opposing group.

In a review of the effect of relative group size on participation in intergroup conflict in mammal, bird, and insect populations, 23 instances (out of a total of 33 records) generally matched evolutionary game theoretic predictions (Van Belle and Scarry 2015): i.e., the likelihood of participation increased when the numeric odds were in favor of the focal group and/or equal between the contestants, or decreased when the odds were against the focal group. However, there was one instance in which participation was more likely when the odds were *against* the focal group (*Colobus guereza*: Harris 2010), which arises when the efforts of the dominant male in a multimale, multifemale group are directed against his intragroup competitors, whereas aggression by the dominant male in a one-male, multifemale group (within the same population) is directed against other groups.

In contrast with game-theoretic predictions, the review identified nine instances in which numeric odds did not predict participation at all (Van Belle and Scarry 2015). One possible explanation for this discrepancy is that contest outcome might be determined by an "uncorrelated asymmetry" (Maynard Smith and Parker 1976) stemming neither from the expected payoffs nor competitive ability, such as a "first come, first priority" convention among bands of feral horses at a water hole (Stevens 1988). Alternatively, perhaps

asymmetries in competitive ability are consistently small and thus overwhelmed by larger asymmetries in motivation. These explanations, however, do not appear to explain the pattern for gray-cheeked mangabeys (*Lophocebus albigena*) at the Ngogo site in Kibale National Park, Uganda (Brown 2014), where no such convention is apparent and group size asymmetries are sometimes substantial. A third possibility is that some aspect of the research or analytical methods prevents the detection of a relative group size effect. For instance, two studies used playback experiments in which the calls of a known, neighboring group were recorded, then broadcast from a speaker placed *ca.* 80 m from the edge of a focal group, and the responses of the latter were monitored to determine whether any males or females approached the speaker (Brown 2014; Crofoot and Gilby 2012). In the study with white-faced capuchins (*Cebus capucinus*), an approach was defined as a binary response of any movement of ≥5 m toward the speaker and the predicted relationship between relative group size and participation was observed (Crofoot and Gilby 2012). For the gray-cheeked mangabeys, however, an approach was defined as a movement of 50 m or more and no effect of competitive asymmetry was detected (Brown 2014). Perhaps the strict definition of an approach in the latter study obscured a positive relationship between relative group size and participation. Alternatively, gray-cheeked mangabey intergroup behavior may be shaped entirely by other factors. Groups of this species were initially described as mutually avoidant, with groups using male long-distance calls to maintain a spatial buffer (Waser 1975, 1976). More recent analyses indicate that groups are willing to confront each other when food resources are limiting and defendable, which was not an issue in the low-density population (0.25 groups/km²) studied at the Kanyawara research site in the 1970s but was a more common circumstance in the high-density population (1.50 groups/km²) studied at the Ngogo site in 2008–2009 (Brown 2013; Brown and Waser 2018). By listening to neighbors' long-distance calls throughout the day, a group can determine the distance and direction to those neighbors, and choose whether to withdraw or approach (Brown 2014); as a result, intergroup interactions at Ngogo appear to be intentional events rather than chance encounters. Close-range intergroup conflicts (where groups are ≤100 m apart) are dramatic affairs that involve much chasing and whoop-gobbling (the long-distance vocalization) by males as well as screaming, intense grunt choruses, and staccato barking by all individuals. Conflicts occur when food patches are scarce and patchily distributed in the environment (Brown 2013). Aggressive participation by female mangabeys does not correspond with food availability but occurs in *ca.* 20% of interactions (Brown 2013), and though they often appear to be attempting to participate, they are threatened and chased away by male group-mates regardless of whether they have a sexual swelling (M. Brown *pers. obs.*). Conflicts occur anywhere in the home range and patterns of aggression do not differ between core and peripheral areas (Brown 2013). The one infanticide observed in this population occurred during an intergroup interaction and was inflicted by a male from a neighboring group (M. Brown *pers. obs.*). No intergroup copulations have been observed (M. Brown *pers. obs.*). Thus despite exhibiting a somewhat low rate of interaction (0.14 interactions/day, averaged across seasons), mangabeys appear to take these conflicts quite seriously and may be strongly motivated to avoid losing access to contested areas.

In this study, I reevaluate the responses of gray-cheeked mangabeys when presented with the threat of a nearby group to determine whether the previous analytical approach (Brown 2014) obscured an effect of relative group size. I use instances in which a male in a study group produced a long-distance vocalization and a listening group was close

enough that they could hear each other's short-range vocalizations (but were not yet close enough to see each other). These are situations in which the calling group represents a potential threat in the near future and allow me to test whether individuals in the listening group chose to approach, ignore, or avoid the calling neighbor. One dataset consists of focal follows conducted during experimental playback trials and is the same as that used in the earlier analysis; the second dataset comes from focal follows conducted immediately after hearing a naturally occurring calling bout from a nearby group. Whereas the previous analysis asked whether at least one individual of each sex made a dramatic approach (≥50 m) toward the calling neighbor (Brown 2014), the current analysis uses all movements, both short/long and toward/away from the calling neighbor, by every focal animal.

Evolutionary game theory posits that contests are initiated, escalated, and resolved by asymmetries in competitive ability and motivation regarding the expected payoffs of winning the contest (Maynard Smith and Parker 1976; Maynard Smith and Price 1973; Parker 1974). If this hypothesis is correct, I predict that individuals will be more likely to retreat when the numeric odds are against them and will approach, or at least hold their ground, when the odds are in their favor. Male gray-cheeked mangabeys are far more active than females during intergroup encounters (Brown 2013), so I predict that male movements will be more positive (toward the caller) than female responses. Among females, those with unweaned infants are vulnerable to infanticide and should be most likely to retreat, even when the odds are in their favor. Females with maximal sexual swellings are guarded by male group-mates (Arlet et al. 2008) so I predict that they will either remain stationary or retreat from a neighbor's calls. There is some evidence that females may lead the group toward neighbors (Brown and Waser 2018) and because females with inflating or deflating swellings often mate with immigrant males (Arlet et al. 2007), these approaches may serve to facilitate copulations with extragroup males; thus I predict that females with swellings attempt to move toward calling neighbors. I also evaluate vertical movements (climbing up to get a better view or descending to hide in the lower canopy or to flee on the ground) to draw a fuller picture of movement responses.

The absence of a group size effect could stem from an inability of the animals to recognize neighbors' calls or to learn their relative sizes. However, earlier studies demonstrated that the whoop gobbles of individual male mangabeys are distinct and elicit predictable reactions according to caller identity, both within the caller's group and in neighboring groups (Waser 1975, 1976, 1977). Moreover, because groups interact approximately once per week in some seasons (Brown 2011) and may hear each other's calls several times each day (Brown and Waser 2018), it is likely that individuals learn whether their group is larger/smaller than specific neighbors. Nonetheless, I consider the possibility that their responses may be more reflective of absolute, rather than relative, size. Group composition at Ngogo is somewhat predictable across months because females are philopatric and, along with immatures, constitute ca. 80% of the group. However, males sometimes disappear for a few days or disperse into neighboring groups (Olupot and Waser 2005) and cause fluctuations in group size that might shift the competitive asymmetry between neighbors. Thus it might be more reliable for individuals to have a general sense that their group tends to be larger or smaller than its neighbors (Arnott and Elwood 2009; Elwood and Arnott 2013). To account for this possibility, I also test whether focal group size is a better

predictor of individual responses than relative group size and predict that individuals in large groups will be more likely to approach a caller than individuals in small groups.

Finally, because the responses of individuals may be influenced by the actions of same-sex group mates with similar resource-defense priorities (Heinsohn and Packer 1995; Meunier *et al.* 2012), I ask whether the likelihood of approach is strengthened when another individual makes a strong approach. Strengthened approaches after a group-mate's close approach would be evidence of social contagion, or even preliminary evidence of cooperative defense; in contrast, a reduced likelihood of approach could be construed as evidence of defection from group-cooperative activities. The potential costs of an approach might be lower for a follower than for an initiator and thus favor apparently cooperative behavior; however, defection might be favored if other individuals have already demonstrated a commitment to confronting the neighbor and additional participants are not needed (Heinsohn and Packer 1995; Nunn and Deaner 2004).

Methods

Data Collection

The data used in this study are part of a larger study on primate intergroup conflicts, for which the methods are described in detail elsewhere (Brown 2011, 2013, 2014; Brown and Waser 2018). In brief, the data come from six adjacent groups of gray-cheeked mangabeys observed from January 2008 through March 2009 (8470 h of observation) at the Ngogo research station (0°29′N and 30°25′E) in Kibale National Park, Uganda. We conducted group counts every month to track the number of adult and subadult females. We recorded less stable aspects of group composition daily: the number of adult and subadult males, which fluctuated for all study groups (Olupot and Waser 2001); females with inflating, peak, or deflating sexual swellings because there is no distinct breeding season in this species (Arlet *et al.* 2007); and unweaned infants (Table I). At half-hourly intervals from dawn until dusk, we recorded the location of the group center-of-mass using the coordinates of a 50 m × 50 m grid superimposed over a trail map.

Each time a bout of long-distance calls was produced by a male group member, we noted the time, context, and number of whoop-gobble calls in the bout. We also made a note of any whoop-gobbles that we heard from neighboring groups, including the time, number of calls in the bout, and the direction from which it was heard; calls are audible to human observers up to 1 km away and may be audible to arboreal monkeys at even greater distances. We typically followed three to six groups on each observation day and thus could often determine whether a neighbor's call came from a specific focal group. Whenever possible, we conducted a 5-min focal follow immediately after a neighbor's call on one male and/or one female in the listening group to record their reactions (females: $N = 59$ focal follows; males: $N = 69$), but only if the observer deemed the calling group to be *ca.* ≤500 m from the listening group. Mangabey group movements change in response to neighbors' calls even when separated by distances up to 1 km (Brown and Waser 2018) and individuals attend to extragroup long-distance calls with great interest (M. Brown *pers. obs.*). Short-range calls (staccato barks, grunts,

Table I Composition of gray-cheeked mangabey study groups at the Ngogo research site in Kibale National Park, Uganda (January 2008–March 2009)

Group	Adult males	Adult females	Subadult males	Subadult females	Sum	Adult females with swellings	Adult females with infants
M1	3.0 (3–4)	8	1–2	1	13.8	0.66/0.65/0.79	1.6
M2	3.1 (2–5)	9	1–3	2	16.9	0.50/0.63/1.04	3.1
M3	3.0 (2–3)	7	1	1	12.0	0.21/0.69/1.04	1.6
M4	1.0 (0–2)	1	0–1	1	3.1	0.02/0.31/0.29	0.0
M5	2.9 (2–3)	5	1–2	1	10.8	0.24/0.31/0.63	0.5
M6	3.8 (3–5)	10	1–2	1	15.8	0.09/0.14/0.24	2.1

"Adult males" presented as daily mean followed by range in parentheses. Daily means of females with sexual swellings (inflating/maximal/deflating) and infants are a subset of "Adult Females."

and screams) can be heard up to *ca*. 300 m away by a human observer and elicit dramatic responses by neighbors in the form of intense vocalizations, staring in the direction of the callers, and rapid horizontal and/or vertical travel (M. Brown *pers. obs.*). We noted the focal animal's initial location, horizontal movement (m) and direction relative to the caller, and whether it climbed up or down at least 1 m (scored as up = 1, down = −1, or no movement = 0), even though most vertical movements were much greater than 1 m. Estimation of vertical distances is made challenging by distance-based perceptual biases and because I was unable to check my estimates against a tape measure, I chose not to attempt more precise measurements of vertical distance. When the caller was another study group under observation, I calculated the distance between the centers-of-mass of the calling and listening groups ("intergroup distance"). We did not include responses to calls from solitary or unknown callers in this analysis, and because groups often heard multiple calls from a particular neighbor per day, we conducted focal follows a maximum of once per day.

We also conducted focal follows after each trial (N = 71) of an auditory playback experiment, which I conducted with all six study groups to measure their reactions to the presence of a simulated nearby group (females: N = 70 focal follows; males: N = 72; see details in Brown 2014). Each stimulus consisted of a single male whoop gobble accompanied by female short-range calls, which I had previously recorded from the focal groups; I did not modify the broadcast sequences by adding or removing any sounds and played each stimulus to a study group only once. The speaker was placed 80 m from the edge of the focal group, within the area of overlap between the two home ranges, ≥2 m above ground, and hidden from any approaching animals. At least three observers were present for each trial: one field assistant operated the speaker while another assistant and I conducted focal follows on two animals. The operator recorded the number and sex of any individuals that moved close enough to be seen from the speaker (considered a "strong approach" in Brown 2014). Individual and group-wide responses to experimental trials were dramatically different from responses to a control stimulus, which was the vocalization of a common understory bird that is neither a food competitor nor predator, and there was no evidence of habituation to the stimuli across trials (Brown 2014). Both field assistants were blind to the experimental condition of "larger" vs. "smaller" neighboring group.

Though the range of responses to natural and simulated calls was identical, there were several important differences in the conditions surrounding these call types. Mangabey males produce whoop gobbles throughout the day (Waser 1977), which allows listeners to track neighbor movements over time; in the playback trials, a single stimulus was played to a listening group with no prior call bouts to signal the approach of the caller (i.e., a surprise encounter; Brown 2014). Second, intergroup distance was kept constant at 100 m in playback trials but ranged from 141 to 640 m during natural calls. Third, playback stimuli contained only one whoop gobble but natural bouts consisted of one to three calls (mean $1.5 \pm$ SD 0.7, $N = 49$ bouts). Finally, playback trials tended to occur in periods without natural calls because the opportunities to conduct a trial were constrained to occasions when neighboring groups were >500 m apart so that the group whose call was being broadcast would not hear its own vocalization (Brown 2014); in contrast, natural calls were most abundant when groups were within close range of each other. Ideally, a multilevel model would account for these differences between natural and simulated calls by including a term for "call source" as a fixed effect. This approach was not possible, however, because of the strong collinearity among call source, intergroup distance, and number of whoop gobbles in the bout, and because the limited number of observations would have resulted in the overfitting of the models; as a result of these constraints, I analyzed the responses to natural and simulated calls separately.

Data Analysis

I began by calculating the mean horizontal and vertical movements of focal animals in each sex- reproductive state condition, in both playback trials and in response to naturally occurring calls, to identify general response patterns (Fig. 1). I then ran several sets of mixed effects regression models and compared among models within a set using the Information Theoretic approach (Burnham and Anderson 2002). In these models, the dependent variable is the horizontal distance moved by the focal animal toward (positive) or away from (negative; including perpendicular movements) the caller, with non-movements scored as zeroes. I included the identities of the focal and calling groups as crossed random effects in all models. The first set of models is designed to determine which, if any, of the control variables best explains variance in the dataset of responses to naturally occurring calls. These control variables are 1) a combined sex and reproductive state variable or just sex, 2) the number of whoop gobbles in the call bout, and 3) the distance between the calling and listening group centers-of-mass. Though I identified six categories for the sex-reproductive state variable (adult females with juveniles, females with unweaned infants, females with inflating sexual swellings, females with peak swellings, females with deflating swellings, and adult males), several of the sexual swelling categories had very low sample sizes (0–3 individuals; Fig. 1) so I concatenated them into three states: females with infants or juveniles; estrous females; and adult males. For the length of the call bout, there was relatively little variation (63% of bouts consisted of just one whoop gobble; 29% consisted of two calls; and the remaining 8% consisted of three calls) so to minimize the degrees of freedom I turned this into a binary variable indicating whether the call bout consisted of one or more whoop gobbles. I calculated intergroup distance using the groups' locations at the nearest half-hour interval and rounded to the nearest
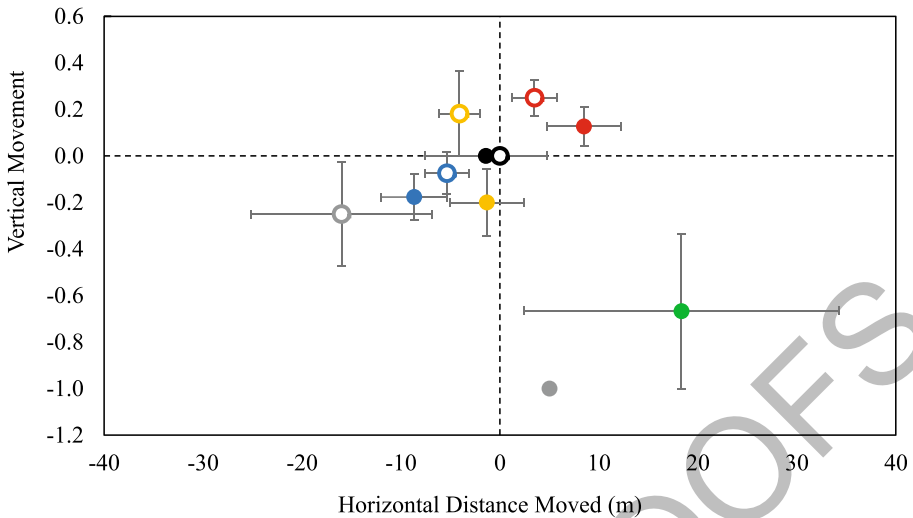
Fig. 1 Mean (± SEM) horizontal and vertical movements by gray-cheeked mangabeys at the Ngogo research site in Kibale National Park, Uganda (January 2008–March 2009) after a naturally occurring call (open circles) or a simulated call during a playback trial (filled circles). Positive and negative values indicate movements toward/away from the caller (x-axis) or up/down in the canopy (y-axis). Color indicates sex and reproductive state: red = adult males (N = 53 responses to natural calls/63 responses to playback trials); blue = adult females with juveniles (27/34); yellow = females with unweaned infants (11/15); green = females with inflating sexual swellings (0/3); black = females with maximal sexual swellings (4/7); gray = females with deflating swellings (4/1).

50 m. I considered all possible combinations of these four variables (but never included "sex" and "sex-reproductive state" in the same model as these are so similar), resulting in 11 models. I calculated the Akaike weight of the models in each set and identified the best-fit models as those having weights within 12.5% of the top-ranked model (Burnham and Anderson 2002; Burnham *et al.* 2011). Two models fell within the "best-fit" criterion: one model contained both sex and intergroup distance while the other contained only intergroup distance. Though sex was not a strong predictor, I included it in the baseline model for comparison with the next set of models for natural calls because sex was a meaningful predictor in other analyses of responses to natural and simulated calls and during physical intergroup contests (Brown 2013, 2014).

For the playback dataset, only "sex" or "sex-reproductive state" was a potential control variable because intergroup distance and number of whoop gobbles were held constant across all trials. The Akaike information criterion (AIC) values of these models were not substantially different so I opted to use the "sex-reproductive state" variable for a more complete understanding of mangabey responses to simulated calls, especially as this dataset was nearly three times larger than the natural calls dataset (see explanation below) and thus less affected by issues of overfitting.

To evaluate the effect of group size on individual movements, I considered two sets of models: one for responses to naturally occurring calls and the other for responses to simulated calls broadcast during playback trials. Each model contained a different measure of group size. I calculated three measures of absolute group size as each sex could, in theory, be persuaded into participation by different aspects of group strength. The first measure of group size is the number of adult males in the group because aggressive encounters among gray-cheeked mangabey groups always

involve male participation but only occasionally include female involvement (Brown 2013). I used the number of adult females in the group as the second measure of group size because female participation may be contingent on the number and behavior of other females. The third measure of group size is the sum of adult and subadult males and females because male and female participation may be scaled to the summed number of potential participants in the group, regardless of their sex. For each of these three variables, I also calculated the asymmetry in competitive ability as the focal group size minus the calling group size. Positive and negative values indicate numeric odds in favor of and against the listening group, respectively. As the calling group size could not be calculated for natural calls made by non-study groups, I limited this dataset to calls made by known study groups. As a result, the number of responses decreased from 128 to 59. In total, there were seven models in each set: the first was a baseline model containing only the control variables; then three models, each with a different measure of absolute group size; then the final three models with different measures of relative group size. As males and females are expected to respond differently, I included an interaction between the sex (or sex-reproductive state) and group size variables. As none of these interactions were significant for the natural calls and thus unnecessarily increased the degrees of freedom in a limited dataset, I reran these models without the interaction terms. Though an information theory approach identifies the best-fit models, these might not have strong biological significance so I also present the variable coefficients and confidence intervals, with the aim of illuminating whether a general pattern of correlations exist between movement responses and group size.

Lastly, I sought to determine whether approaches toward calling neighbors were socially contagious, i.e., whether an individual would be more likely to approach if others in its group made a strong approach. The assistant operating the speaker took note of any strong approaches ($\geq$50 m) in response to playback stimuli but this was not possible after natural calls, so this analysis was limited to the playback dataset. I used the model with the lowest AIC from the previous step and included a term for "strong approach by at least one individual of the same sex," because same-sex group-mates are most likely to have the same motivations for approaching. I excluded focal responses in which the individual moved $\geq$50 m toward the speaker, as these were the strong approaches that I expected to affect the responses of other individuals; doing so reduced the sample size from 142 to 131 observations. Though it was not significant in the earlier set of models, I tested the interaction between group size and the focal animal's sex-reproductive state to determine whether responses by certain classes of individuals changed as a function of group size in the context of close approaches by other individuals. This interaction was not significant so I excluded it from the final model. I used a likelihood-ratio test to determine whether adding the "other approach" term significantly improved model fit.

I standardized all continuous variables by centering about the mean and dividing by two times the standard deviation, as recommended for interpreting effect sizes when some of the predictors are binary (Gelman 2008). I checked plots of the standardized residuals against the predictor variables to rule out the possibility of systematic bias in the patterning of residuals, and found all variance inflation factors to be <2, indicating that multicollinearity was not an issue (Tabachnick and Fidell 2007). I conducted all analyses in STATA v12 (StataCorp LP, College Station, TX).

Ethical Note

This study adhered to the Principles for the Ethical Treatment of Primates of the American Society of Primatologists. No animals were captured or handled for this study. All observational and experimental manipulations conformed to protocols reviewed and approved by the Columbia University IACUC (#AC-AAAA8112), the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Uganda Office of the President. This study adhered to Ugandan legal requirements. I declare no potential sources of conflict of interest.

Results

In general, males moved toward a calling neighbor group and into a higher canopy level, presumably in an effort to acquire visual information about the caller, both after natural and simulated long-distance vocalizations (Fig. 1). Females with juveniles or infants moved away from callers and down toward the ground (except for females with infants after simulated calls, which moved higher within the canopy). Females with inflating or deflating estrous swellings exhibited the most variable responses, though

Table II Models evaluating the effect of control variables on gray-cheeked mangabey movement responses at the Ngogo research site in Kibale Park, Uganda (January 2008–March 2009), after hearing natural or simulated calls from a neighboring group

Stimulus type Model	Overall model AIC	w_i
Natural calls ($N = 59$)		
Sex-reproductive state + bout length + intergroup distance	472.95	0.03
Sex + bout length + intergroup distance	471.41	0.09
Sex-reproductive state + bout length	475.95	0.01
Sex + bout length	474.02	0.03
Sex-reproductive state + intergroup distance	471.78	0.08
Sex + intergroup distance	*470.16*	*0.23*
Bout length + intergroup distance	471.35	0.13
Sex-reproductive state	474.24	0.03
Sex	472.29	0.10
Bout length	473.61	0.05
Intergroup distance	*470.67*	*0.23*
Simulated calls ($N = 142$)		
Sex	1325.36	
Sex-reproductive state	1325.65	

Best-fit models are identified in bold italics.

the small number of such observations weakens confidence in the observed patterns: they moved down and away from real callers, but toward simulated callers. After hearing a natural call, all animals tended to retreat from neighboring groups that were <500 m away and to approach more distant groups (Table II), matching the pattern found in earlier analyses (Brown and Waser 2018; Waser 1975, 1976, 1977).

In response to naturally occurring calls, focal animals in small groups retreated, while those in large groups occasionally approached the caller (Table III, Fig. 2a). Nearly all measures of group size correlated positively with focal animal movements and had AIC scores lower than the null model, indicating the robust biological significance of group strength on individual responses to an extragroup threat. Though only one model (containing absolute total group size) fell within the confidence set of best-fit models, the patterning of the AIC values indicates that both absolute and

Table III Models evaluating the effect of group size on gray-cheeked mangabey horizontal movements after hearing a natural or simulated call from a neighboring group at the Ngogo site in Kibale National Park, Uganda (January 2008–March 2009)

Model	Model AIC	w_i	Group size coefficient and 95% CI
Natural calls ($N = 59$ responses)			
<no group size predictor>	470.16	0.01	—
Absolute size: adult males	467.78	0.02	*6.19 (0.63, 11.75)*
Absolute size: adult females	466.48	0.03	*8.67 (2.86, 14.47)*
Absolute size: adults + subadults (best fit)	461.12	0.58	*9.83 (4.68, 14.97)*
Relative size: adult males	471.83	0.00	1.72 (−3.85, 7.29)
Relative size: adult females	464.54	0.08	*9.34 (3.56, 15.11)*
Relative size: adults + subadults	461.92	0.29	*10.02 (5.14, 14.90)*
Simulated calls ($N = 142$ responses)			
<no group size predictor>	1325.36	0.06	—
Absolute size: adult males[a]	1324.38	0.07	
Absolute size: adult males (best fit)	1321.49	0.39	*11.57 (2.64, 20.51)*
Absolute size: adult females[a]	1323.90	0.10	
Absolute size: adult females	1324.50	0.09	8.94 (−0.88, 18.76)
Absolute size: adults + subadults[a]	1326.31	0.03	
Absolute size: adults + subadults	1325.57	0.06	7.27 (−2.56, 17.11)
Relative size: adult males[a]	1327.87	0.01	
Relative size: adult males	1324.26	0.10	9.10 (−0.48, 18.67)
Relative size: adult females[a]	1327.96	0.01	
Relative size: adult females	1325.64	0.05	6.58 (−2.50, 15.65)
Relative size: adults + subadults[a]	1329.41	0.01	
Relative size: adults + subadults	1326.00	0.04	6.21 (−3.25, 15.67)

Best-fit models have the lowest AIC values. Group size variables with 95% confidence intervals not crossing zero are in bold italics. Each model also contains random effects and control variables (natural: sex, intergroup distance; simulated: sex-by-reproductive state).

[a] Model includes an interaction term between the group size and control variables; the main effect of group size is not presented for these models because of the presence of the interaction term.
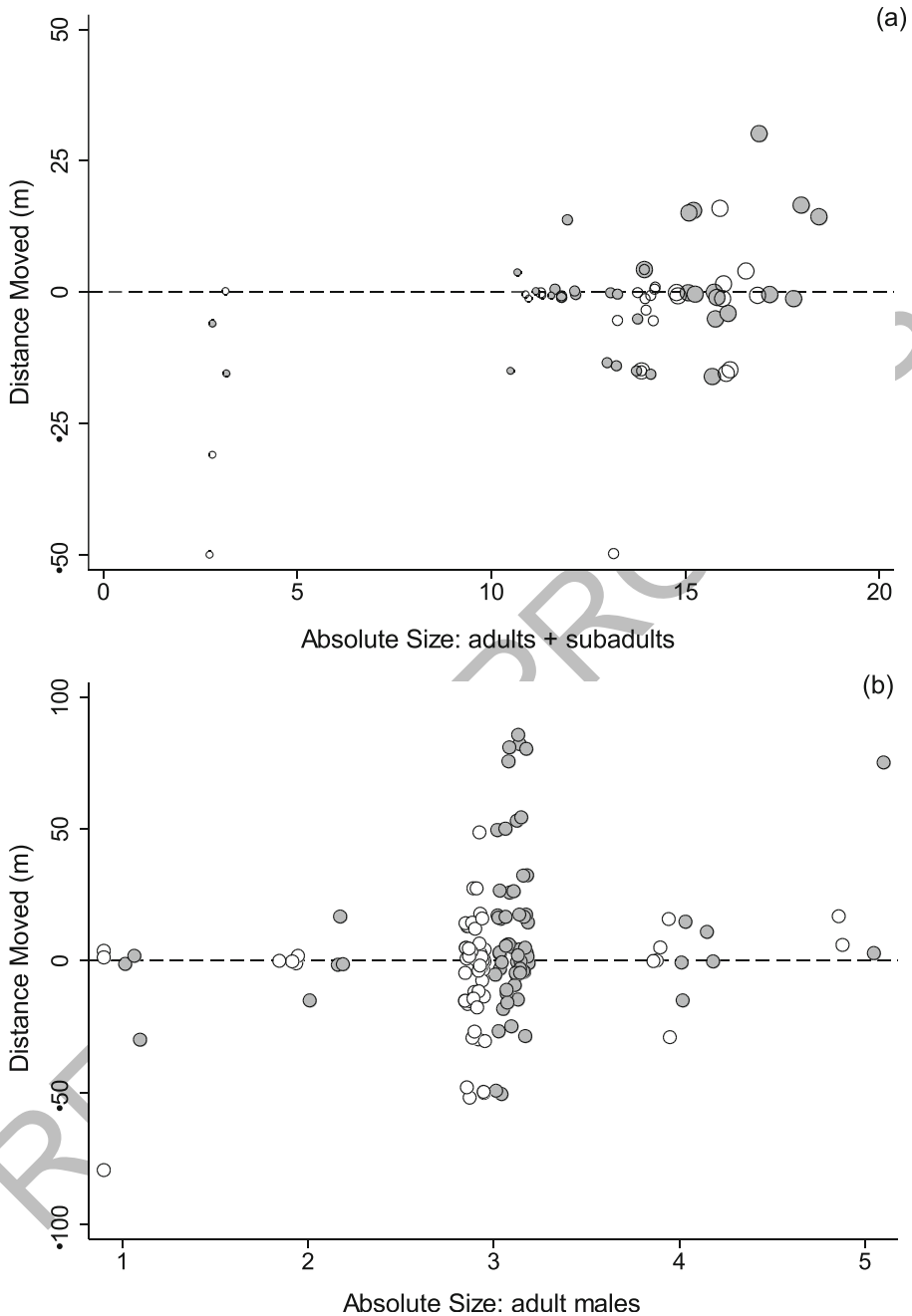
Fig. 2 Movement responses of female and male (white and gray circles, respectively) gray-cheeked manga-beys at the Ngogo site in Kibale National Park, Uganda (January 2008–March 2009) as a function of group size. (a) Responses to naturally occurring calls; marker size indicates absolute group size (small = 2–11 individuals; medium = 12–14; large = 15–19). (b) Responses to playback stimuli; points are jittered and male and female responses are placed next to each other for clarity.

relative measures of *total* group size were better predictors than the number of adult females, which in turn was a better set of predictors than the number of adult males.

In response to a simulated call, only the absolute number of adult males correlated with individual movement responses (Table III). Individuals in groups with intermediate numbers of adult males retreated from and approached the speaker at roughly equal frequencies (Fig. 2b); the tendency to retreat was most pronounced when groups contained only one male, and a tendency to approach occurred when groups contained five adult males.

When at least one same-sex individual made a strong approach toward a simulated neighboring group, movements by other animals were more positive (coefficient = 8.63, SE = 3.57; Fig. 3), indicating a degree of social contagion in the likelihood of approaching an extragroup threat. This model was a significant improvement over the version without the "other approach" term ($\chi^2_1 = 5.23$, $P = 0.02$). The group size term was no longer a significant influence on travel responses in the presence of the "other approach" term (coefficient = 6.77, SE = 3.47).

Discussion

When evaluating the full range of movement responses, I find that group size predicts gray-cheeked mangabey behavior after hearing a neighboring group's long-distance call, particularly when groups are >100 m apart. As predicted by evolutionary game theory, individuals in smaller groups retreated from a larger neighbor while those in larger groups exhibited more variable responses. This result contrasts with an earlier
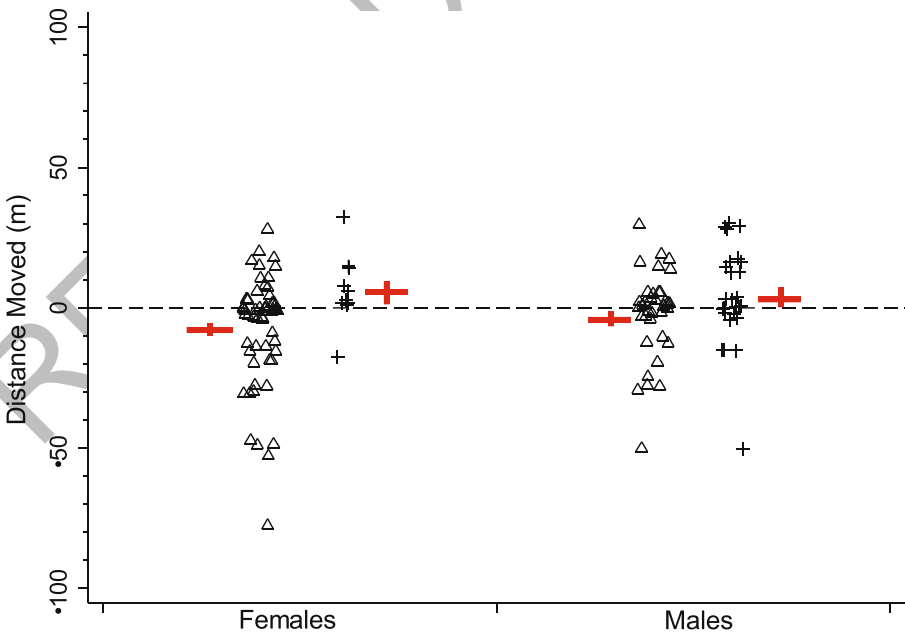

Fig. 3 Horizontal movements by focal gray-cheeked mangabeys at the Ngogo site in Kibale National Park, Uganda (January 2008–March 2009) during playback trials when others of the same sex do (crosses) or do not (open triangles) make a close approach to the speaker. Mean ± SE indicated by red "+" signs.

analysis (Brown 2014) in which the movements of groups that were within close range (≤100 m) were not affected by group size, but instead by the expected resource-related payoffs of winning an intergroup conflict. In the current analysis, the effect of group size during close-range interactions is again nullified, but by social contagion.

The fact that group size predicts mangabey behavior at longer intergroup distances (natural calls: 150–650 m) but not at close range (playback trials: 100 m) is unusual and may result from the extended, sequential nature of their intergroup interactions. The distances at which they can hear loud calls, then hear short-range vocalizations, and then establish visual contact are stages in which mangabeys can assess their relative resource-holding potential and motivation to gain or maintain access to a resource (Brown and Crofoot 2013), and thereby choose whether to continue approaching a neighbor or to avoid a physical contest. It appears that whole-group size rather than adult male membership is relevant at longer intergroup distances (Brown and Waser 2018), but when food is limiting and defendable and groups have consequently chosen to make a close approach, further escalation is determined by the expected payoffs (Brown 2014) and by socially contagious behavior (this study). Additional study is needed to determine whether this contagion is proportional to the number of group-mates that participate in intergroup conflicts (Zhao and Tan 2010), or whether the only meaningful predictor is a strong approach by a single individual (Cords 2002; Heinsohn and Packer 1995).

In an earlier analysis, Brown and Waser (2018) found that the relative number of males in the listening group did not predict group-wide movement after hearing a naturally occurring call from a neighboring group—a finding replicated here in the context of individual movements. Adult males were expected to determine group travel direction because they are the primary participants in close-range intergroup conflicts (Brown 2013) and often herd group-mates away from these conflicts (M. Brown *pers. obs.*). This discrepancy in the role played by males during close-range versus long-distance interactions points to the necessity of testing multiple measures for any one variable, and doing so independently for each contest phase (e.g., contest initiation, escalation, and outcome; Harris, 2010). Moreover, the group size effect in mangabeys could only be detected when all horizontal movements, rather than only strong approaches of ≥50 m, were evaluated. It remains to be determined whether the other eight studies lacking a group size effect (Van Belle and Scarry 2015) would also conform to game-theoretic predictions if different analytical methods were employed. For instance, Hopkins (2013) studied mantled howler monkeys (*Alouatta palliata*) and found no effect of group size on group movements. However, only "sustained travel bouts" lasting at least 20 min were considered to be a response to a call from a neighboring group, rather than measuring movements of all lengths. In addition, group dominance rank predicted movement responses, and because rank correlates strongly with the number of males in the group, there appears to be an unrecognized effect of male group size on movement responses.

Though group size clearly affects whether a listener chooses to approach or retreat from a neighbor, its predictive power is greater for individuals in smaller groups (who retreat) than in larger groups (who both retreat and approach). This highlights two underappreci-ated aspects of evolutionary game theory. First, the theory does not necessarily predict that a larger group will be aggressive toward a weaker competitor. Instead, it predicts that the smaller group will retreat while the larger group will not; a larger group may hold its ground, rather than approaching, and still conform to game-theoretic predictions (Elwood

and Arnott 2012; Maynard Smith and Parker 1976; Maynard Smith and Price 1973; Parker 1974). There is a tendency in the primate literature to focus on approaches and aggression (Willems and van Schaik 2015; Wrangham 2018) rather than retreating or remaining in place (cf. Crofoot and Gilby 2012), which prevents accurate testing of evolutionary game theoretic principles. For instance, when conducting the playback trials there were several instances in which a focal group that had been feeding in a large tree crown stopped abruptly after hearing the broadcast call (M. Brown pers. obs.). Most of the group then moved to the edge of the crown, facing the speaker, and waited while making agitated vocalizations and peering in that same direction. This appeared to be a defensive positioning around a valuable food source and contrasted sharply with instances in which group members either approached or ran away from the speaker. Thus by holding their ground, the group appeared to be ready to defend the resource from a perceived competitor. These observations indicate the need for a more nuanced consideration of primate intergroup encounters, taking into account the pre-conflict activity (Brown 2014; Markham et al. 2012).

Second, in the context of intergroup contests, the power of game theory to predict individual behavior within larger groups is potentially weakened by a collective action problem (Hawkes 1992; Watts and Mitani 2001). In other words, an individual in a larger group might retreat because its group-mates are approaching or holding their ground; by defecting, the retreating individual bears none of the costs associated with intergroup conflict but reaps the benefits of being in a larger group. However, there was no evidence of a potential collective action problem among gray-cheeked mangabeys. Both males and females made closer approaches toward a competing group if at least one same-sex individual made a close approach, whereas inaction or retreat would be more likely if a collective action problem existed. These results directly contradict the interpretations of Willems and van Schaik (2015), who predict the presence of a collective action problem in populations like the Ngogo gray-cheeked mangabeys because groups live in highly overlapping home ranges and contain multiple individuals of the dominant sex (Brown 2013).

Despite the absence of a collective action problem, the fact remains that some individuals in larger mangabey groups retreated from a calling neighbor. Though group-mates may be motivated to defend a shared resource, individuals within a group and of the same sex may also experience very different degrees of motivation based on rank, age, or access to the contested resource (Kitchen and Beehner 2007; Watts and Mitani 2001). Thus some individuals may be highly motivated to approach a nearby neighbor to maximize the benefits associated with winning the contest (a small cost/benefit ratio), while others might be more motivated to minimize the costs (a large cost/benefit ratio; Enquist and Leimar 1987; Hurd 2006). Costs that favor a retreat might be a lack of energy to engage in conflicts; the presence of a young infant vulnerable to infanticide (Harris and Monfort 2003; Vogel and Fuentes-Jimenez 2006); and aggression by male group-mates toward females to prevent any contact with extragroup males (Byrne et al. 1987). Benefits that stimulate an approach might be enhanced access to contested food resources (Brown 2013); greater access to estrous female group-mates, which may prefer to mate with males that demonstrate a commitment to defending resources (Fashing 2001); and acquiring information about the composition and motivation of competing groups, which may lead to migration opportunities (Lazaro-Perea 2001).

Variability of individual movements in large groups may represent the consensus-building process and indicate a greater range of conflicting motivations than is present in smaller groups. Group travel direction is sometimes decided by a majority rule in which individuals "vote" with short movements in their preferred direction or other gestures of intent (Strandburg-Peshkin *et al.* 2015; Walker *et al.* 2017). Further study is needed to measure the costs and benefits perceived by individual animals, and to determine whether this ratio predicts behavior in competitive contexts.

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