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Patch Occupation Time Predicts Responses by Grey-Cheeked Mangabeys (*Lophocebus albigena*) to Real and Simulated Neighboring Groups

Michelle Brown

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Abstract When two social groups are close enough to hear each other's short-range vocalizations but not yet close enough to see each other, they can choose whether to approach to initiate a direct contest. In this study, I evaluated whether expected payoffs and group resource-holding potential affected the likelihood of approach toward a neighboring group during naturally occurring intergroup interactions and experimental playback trials by grey-cheeked mangabeys (*Lophocebus albigena*). Females approached calling groups at low rates, and only if males did so as well. Groups that had recently arrived (≤ 30 min) at the interaction location were more likely to approach than groups that were in the interaction location for >30 min. Site residency likely indicates the degree of short-term, local resource exploitation, and explains this pattern of patch defense. There was no evidence that mangabeys defended home range core or peripheral areas, that males defended female mates, or that infant defense affected the likelihood of approach. Surprisingly, resource-holding potential had no effect on patterns of contest initiation, but may influence other aspects of intergroup contests. The unexpected importance of payoff asymmetries, relative to asymmetries in resource-holding potential, points to the need for an expanded theoretical framework.

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Introduction

Evolutionary game theory (Maynard Smith 1974; Parker 1974) posits that animal contests are settled by asymmetries, e.g., in competitive ability (resource-holding potential [RHP]; Zhao and Tan 2010), the fitness-related benefits to be gained by winning the contest (payoffs; Harrison 1983; Pride *et al.* 2006; Putland and Goldizen 1998), or both RHP and payoffs (Crofoot *et al.* 2008; Harris 2010; Kitchen *et al.* 2004). Weaker or less motivated contestants are generally reluctant to initiate contests that they are likely to lose, whereas stronger or more motivated contestants do not avoid competitors (Furrer *et al.* 2011; McComb *et al.* 1994; Wilson *et al.* 2012). Vocalizations are an important mode of communication between animal groups in the initial stages of a contest (McGregor 1993; Waser and Wiley 1979), and the reactions they elicit from neighbors—approaching, fleeing, or not responding—help to reveal the nature of the relationship among groups. To an extent that varies across species and populations, these call-and-response sequences are modulated by the context in which the calls are produced and heard (Furrer *et al.* 2011; Heinsohn 1997).

The payoffs gained through intergroup contest competition are measured in terms of access to resources, such as feeding sites (Mitani 1985; Peres 2000; Wich *et al.* 2002). If groups initiate contests as a means of defending access to food, approaches should exhibit a strong spatial patterning, corresponding with the locations of specific food patches (Hypothesis 1), the core of the home range (Hypothesis 2), or the entire range (Hypothesis 3; Brown 2013). Defense of food patches should result in approaches occurring most often during periods of low overall food abundance, when feeding sites are widely dispersed, and in locations with relatively large quantities of food, i.e., when food is limiting and monopolizable (Prediction 1a; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980). In addition, a group that has recently arrived at a food patch and has not yet fully exploited it should be more likely to approach than a group that has fed on the patch exhaustively (Prediction 1b; Houle *et al.* 2006). Defense of core areas should result in approaches occurring most often when the interacting groups are in the center of the focal's range, rather than at the periphery (Prediction 2; Crofoot and Gilby 2012; da Cunha and Byrne 2006; Harris 2006; Kinnaird 1992; Mitani 1985). Defense of the entire home range should result in an equally high frequency of approaches in the core and periphery, though the number of opportunities will likely be higher in the periphery (Prediction 3a); however, if the calling group is outside of the focal group's range, the latter should not approach (Prediction 3b; Peres 2000; Robinson 1979). Because the context considered here is the initiation of close-range interactions, the distance between the focal and calling groups is assumed to be short and relatively uniform.

Food-related payoffs may also take the form of infant defense, if intergroup infanticide is used as a means of intimidating neighboring groups to gain access to valuable resources (Hypothesis 4; Harris and Monfort 2003). If males and females attempt to protect vulnerable infants, both sexes should be less likely to approach neighboring groups when unweaned infants are present in the focal group than when such infants are absent (this implies that approaches are

necessitated by the defense of some other resource, such as food patches; Prediction 4).

For males, payoffs may also be measured in terms of access to fertile female mates (Dunbar 1988; Wich and Nunn 2002). If such access is ensured by aggressively preventing extra-group males from immigrating or temporarily interacting with female group mates (Hypothesis 5), male approaches should occur *more* often when estrous females are present than when they are absent (Prediction 5; Kitchen *et al.* 2004). Conversely, if males ensure their access to fertile females by aggressively preventing female group mates from interacting with extra-group males (Hypothesis 6), male approaches should occur *less* often when estrous females are present (Prediction 6); in this case, because male coercion inhibits female participation, female approaches should also occur less often when estrous females are present.

Lastly, group RHP is likely to affect patterns of contest initiation (Hypothesis 7), and should be approximated by the number of group members in the age–sex classes that participate aggressively (Kitchen 2003; Zhao and Tan 2010). If the resource at stake is valued by both groups and asymmetries in group RHP are the primary determinant of group responses, then call-and-response sequences should be invariant for each group dyad; in other words, for a particular dyad, the larger group will always approach and the smaller group will never approach (Prediction 7a). Alternatively, if RHP merely modulates the effect of payoff asymmetries (Crofoot *et al.* 2008), it should result in a general tendency for larger groups to approach at higher frequencies than smaller groups, but smaller groups should approach when the payoff asymmetries are strongly in their favor (Prediction 7b).

In this study, I used a game-theoretic approach to examine responses by grey-cheeked mangabeys (*Lophocebus albigena*) to calls from real and simulated neighboring groups. I focused on interactions with nearby groups, i.e., where the calling group was close enough to be considered an imminent threat, but could not yet be seen by the listening group, to evaluate the conditions under which the listening group would approach more closely to initiate a contest. Though mangabeys at low density (0.25 groups/km²) exhibited strong avoidance of neighboring groups (Waser 1975, 1976, 1977), mangabeys at higher density (1.50 groups/km²) interact at close range nearly every week in certain seasons, and do not exhibit consistent patterns of avoidance (Brown 2011). In addition, though I have demonstrated elsewhere that mangabey males participate aggressively in intergroup interactions (IGIs) to defend specific food patches (Brown 2013), it is possible that patterns of contest initiation and aggressive escalation differ.

Methods

Study Species and Site

With a team of local field assistants, I studied six habituated grey-cheeked mangabey groups at the Ngogo site in Kibale National Park, Uganda. Mangabey groups are typically multi-male, multi-female assemblages that may include as many as 27 independently locomoting individuals (Table 1). Males exhibit primary and secondary dispersal, whereas females remain in their natal groups (Olupot 1999). At Ngogo,

mangabeys spent the majority of their time in the tree canopy (*pers. obs.*), where they fed on fruit (79% of the plant diet), young leaves (14%), flowers (6%), and cambium (1%); they also spent much time foraging for sessile insects (Brown 2011).

The home range of each focal group (95% minimum convex polygon, mean $1.54 \pm \text{SD } 0.29 \text{ km}^2$, $N = 6$ groups) overlapped with the ranges of at least three other focal groups, and the area of overlap per pair of groups was substantial (mean $0.34 \pm \text{SD } 0.31 \text{ km}^2$, $N = 13$ pairs; [Electronic Supplementary Material \[ESM\]](#)). Mangabey long-distance calls (“whoop gobbles,” produced by adult males in response to neighboring groups, eagle attacks, tree falls, and other loud sounds; Waser 1977; *pers. obs.*) are audible to a human observer at least 1 km away in closed forest (Waser 1977), and are produced throughout the day (mean $9.7 \pm \text{SD } 0.2$ calls per 11-h day, $N = 891$ group-days). Owing to the large degree of range overlap and the distance over which whoop gobbles are audible, groups appeared to be within auditory contact of at least one other focal group on a majority of observation days.

Data Collection

We followed three groups throughout the study and the remaining three groups for shorter periods (Table I). We followed the groups during observation periods of (mean) $8 \pm \text{SD } 1 \text{ d}$ ($N = 27$ periods), separated by periods of *ca.* 10 d. On each observation day, one or two assistants followed each group (up to six groups simultaneously), recording data from 07:30 to 18:30 h. I moved from group to group, monitoring data collection and conducting playback trials. We recorded the location of the estimated center of mass of the group at 10-min intervals using a $50 \text{ m} \times 50 \text{ m}$ gridded map of the trail system (referred to hereafter as location scan); pinpointing the center-of-mass was facilitated by the fact that mangabeys constantly communicate with each other with various types of grunts (*pers. obs.*), and group spread approximates one quadrat (mean $50 \pm \text{SD } 20 \text{ m}$, $N = 15,219$ location scans).

We conducted group scan samples at 30-min intervals, during which an observer walked under the group and recorded the activity of half of the adults and subadults within a 5-min window. The observer watched each individual for 5 s and then recorded its

Table I Observation effort, number of location scans, and composition of each grey-cheeked mangabey group at the Ngogo site in Kibale National Park, Uganda, from January 2008 to March 2009

Group	Observations		Location scans	Group composition					
	Months	Hours		AM	AF	SM	SF	JV	Total
M2	Jan 08–Mar 09	1,736	9,837	2–4	9	2–3	2	7–9	22–27
M6	Nov 08–Mar 09	780	4,462	2–4	10	1	1	6–7	20–23
M1	Jan 08–Mar 09	2,023	11,302	3–4	8	1–2	1	6–7	19–22
M3	Jan 08–Mar 09	2,015	10,934	2–3	7	1	1	7–8	18–20
M5	Jun 08–Mar 09	1,429	7,964	2–3	5	1–3	1	4–5	15–17
M4	May 08–Mar 09	487	2,619	1	1	0	1	1	4

AM = adult males; AF = adult females; SM = subadult males; SF = subadult females; JV = juveniles. Groups are arranged in order of descending size.

activity on the sixth second; if the subject was looking for or ingesting plant parts, the observer recorded its activity, as well as the quadrat in which the plant was located (hereafter feeding quadrat), species, diameter at breast height (i.e., at 130 cm above the ground), and part eaten (fruit, flower, young leaf, mature leaf, cambium, or pith).

Resident males sometimes left and nonresident males sometimes visited the group for short periods (Olupot and Waser 2005; *pers. obs.*), so we counted them every day. We also made a daily record of the number of females with sexual swellings (Arlet *et al.* 2007). We conducted group counts in each observation period, where multiple observers counted and identified the age–sex class of individuals (following Chalmers 1968) as they moved in a linear fashion through an opening in the canopy. Clinging infants were not included in the group counts (Table 1) because they did not participate in IGIs (*pers. obs.*).

Naturally Occurring IGIs

We were generally able to anticipate the beginning of an interaction using the groups' long-distance and short-range calls (grunts, loud grunt choruses, and staccato barks), which can be heard up to 300 m away and are produced by all age and sex classes (*pers. obs.*). An IGI began when we estimated the nearest edges of two groups to be ≤ 100 m apart, regardless of whether either group exhibited aggressive behavior. The IGI ended when the groups' edges were > 100 m apart. These thresholds were based on the typical distance at which all group members began to face the neighboring group, and at which focal group members exhibited strong behavioral reactions toward the neighboring group, i.e., chasing or attacking. A more general analysis of call-and-response sequences, including interactions at longer intergroup distances, will be presented elsewhere (Brown and Waser, unpub. data).

During an IGI, one person watched the focal group's males, a second person watched the focal group's females, and a third person (if present) watched the leading edge of the opposing group. Immediately after the IGI, we recorded the location of the interaction and the degree of participation by each sex, i.e., sitting at the front edge of the focal group, running into or chasing the neighboring group, or attacking members of the neighboring group.

Experimentally Simulated IGIs (Playback Trials)

I recorded calls from the study groups using a Sennheiser ME66 short shotgun microphone (Sennheiser Electronic Corporation, Old Lyme, CT) and a Marantz PMD-660 portable digital recorder (Marantz America, LLC, Mahwah, NJ) and prepared stimulus recordings using Raven Lite 1.0 (Cornell Lab of Ornithology, Ithaca, NY). I used natural sequences of male and female calls and did not alter them digitally by removing or inserting vocalizations. The calls were intended to simulate the presence of an entire group and consisted of both male and female vocalizations. Each stimulus sequence was mean $34 \pm \text{SD } 9$ s and consisted of a fade-in period (*ca.* 3 s), a single whoop-gobble and multiple calls from females and juveniles (grunts, intense grunt choruses, and/or staccato barks), and a fade-out period (*ca.* 3 s). I standardized the volume of each stimulus call sequence using a digital sound pressure meter (Radio Shack Corporation, Fort Worth, TX) so that the “whoop” portion of the

male call was 75 dB at 5 m from the sound source (as per Waser and Waser 1977). To avoid one main source of pseudoreplication (McGregor *et al.* 1992), I played a particular call to a focal group only once, e.g., I played nine calls from group M2 to group M1, and each time I used a different recording.

I placed the speaker 80 m from the edge of the focal group, in the direction appropriate for the calling group. An assistant played the call when signaled via walkie-talkie. Calls were broadcast from a CD player connected to a Fender Passport P10 speaker (Fender Musical Instruments Corporation, Scottsdale, AZ), elevated ≥ 2 m above ground using a Shure telescoping microphone stand (Shure Incorporated, Niles, IL) or by hanging the speaker from a tree branch. Immediately after the call ended, the assistant disassembled and hid the playback apparatus. The assistant then identified any individuals that came within view of the speaker's original location. Another assistant and I observed the focal group for 15 min, one observing the females and the other observing males, and we also recorded whether any male or any female came within visual contact of the speaker. We did not conduct group scans during playback trials, but we did continue to record location scans at 10-min intervals.

I conducted playback trials with the groups only if all of the following conditions were met: there were ≥ 4 d between trials; the focal group had not already had an IGI that day; the group whose call I played was ≥ 1 km from the focal group, so that the calling group would not react to its own vocalizations (Waser 1977); no other groups were within 500 m of the focal group or speaker, to ensure that other groups would not respond with a rapid, close approach; and the focal group had not been traveling for ≥ 10 min. Groups appear capable of recognizing the calls of specific individuals both within and between groups (Waser 1977), so I assumed that groups would recognize the calls of neighbors. I observed groups intruding deeply into neighbors' ranges on a number of occasions, so in a few playback trials, I placed the speaker slightly outside the calling group's typical ranging area.

I also conducted control trials to determine whether the playback setup, rather than the experimental stimulus, was responsible for eliciting approach responses. I used the call of an eastern black-headed oriole (*Oriolus larvatus*)—a commonly heard bird that is neither a predator nor food competitor to grey-cheeked mangabeys (*pers. obs.*)—as the control call. Each control stimulus was mean $33 \pm \text{SD } 4$ s, and like the experimental stimulus, included fade-in and -out phases. Neither sex approached the speaker during these trials; the lack of response to control trials indicates that approach responses during experimental trials were reactions to the experimental stimuli and not to the playback setup.

Comparison of IGIs and Playbacks

The experimental playback trials differed from natural IGIs in the sequence of events leading up to the interaction. Before natural IGIs, groups typically exchanged several calling bouts over a number of hours (Waser 1977; *pers. obs.*), but no such exchange of calls occurred in the hours preceding a playback trial. During periods with many IGIs, it was usually impossible to conduct playback trials because groups spent the majority of their time < 500 m apart and could have heard their own calls broadcast to neighboring groups. Thus, I was largely limited to conducting playback trials during periods when groups tended to be more widely spaced. In addition, before conducting a playback

trial, I waited until the group had been resting for >10 min; consequently, I conducted relatively few playback trials when the focal group had been in the playback location for short periods. Nonetheless, these differences between naturally occurring IGIs and playback trials ultimately strengthened the analysis because they revealed mangabey responses under a broad set of environmental conditions.

Data Analysis

Because males and females may have different motivations for approaching a neighboring group (Harris 2007), I evaluated their responses separately. I categorized male and female responses during playbacks and IGIs as either “stationary” or “approach” (where an individual moved far enough that it could be seen by the assistant operating the speaker). Individuals of a particular sex may experience varying degrees of motivation, so some individuals may remain stationary while others approach. Because the hypotheses under consideration address male and female resource defense in a general way, I considered an approach by at least one individual per sex to be a sufficient indicator for testing the predictions. Withdrawal responses are not addressed by the predictions and would have required extra observers to be placed at the rear of the group, which was not feasible during this study.

The methods I used to calculate food abundance, feeding site distribution, and feeding patch size are described in detail elsewhere (Brown 2013). Briefly stated, I measured food abundance as the summed availability of fruits, flowers, and young leaves in a given observation period, where a species’ availability was the product of its abundance (stem density), stem size (basal area), and percentage of stems with food (calculated from feeding observations). The stem density was calculated using data from 158 50 m × 50 m botanical plots, and basal area from the diameter at breast height of trees in which the mangabeys fed. Feeding site distribution was the variance-to-mean ratio of the distance between each pair of feeding quadrats in an observation period for a particular group. Ratios <1 indicated uniform distributions, = 1 indicated random distributions, and >1 indicated clumped distributions. As abundance and distribution were highly correlated ($y = 5.78x^{-0.96}$, $R^2 = 0.71$), I created a composite variable by subtracting 1 from each distribution score (so that uniform distributions were negative, random distributions were 0, and patchy distributions were positive) and multiplying by the abundance score.

Whereas food abundance and distribution measured food availability throughout the home range, feeding patch size was specific to the interaction location. Patch size was the average basal area of recently fed-upon food trees in the interaction location, i.e., the center-of-mass quadrat and the surrounding two layers of quadrats, weighted by the stem density of each food species.

My field observations, as well as examination of box plots, indicated that recently arrived groups were more likely to approach than sedentary groups, so I transformed site occupation time into a binary variable to indicate whether the focal group had been in the interaction location (the interaction quadrat and the two surrounding layers of quadrats) for a short or long period ($\leq$ or >30 min) before the interaction. Site occupation time was thus a proxy for feeding opportunity, where long occupation times likely indicated that the focal group had fully exploited the local resources.

Using the 10-min location scans, I calculated the home range of each group as a set of concentric minimum convex polygons in 10% increments in Biotas (Ecological Software Solutions, Inc.) except for the outermost layer, which was a 5% polygon. The locations of the focal and calling groups within their own home ranges at the beginning of the interaction (focal group zone and neighboring group zone) were coded from 1 to 10, according to the zone in which they were located.

The number of estrous females in the group consisted of females with inflating, peak, and deflating swellings (Arlet *et al.* 2007) that were present on the day of the interaction, and unweaned infants as the number of offspring that were consistently carried between tree crowns by adult females.

I considered three separate measures of group RHP: relative group size, as focal group size (adults and subadults) minus neighboring group size; focal group size; and adult males within the focal group, because they participated in all aggressive interactions, whereas females participated in relatively few aggressive interactions (Brown 2013).

Statistical Analyses

To determine if males or females became habituated to the playback trials, I compared sex-specific movement responses to trial order using nonparametric Wilcoxon tests. I then compared the conditions under which IGIs and playback trials occurred to confirm that they overlapped to some extent, but also represented somewhat divergent states for the variables of interest (e.g., home range location and relative group size). Because many of the predictors were extremely non-normally distributed, even after transformation, I used Wilcoxon tests for this comparison. To determine whether the larger group in a dyad always or sometimes approached (Prediction 7a vs. 7b), I calculated the percentage of interactions in which each group approached a particular neighbor.

To simultaneously test the seven hypotheses against male and female responses, I conducted multilevel logistic regressions with the identity of the focal and opposing groups as crossed random effects (Rabe-Hesketh and Skrondal 2008), which allows for the inclusion of observations on both groups during a particular IGI. I created a set of 18 *a priori* global models, each of which included all or most of the predictor variables (Table II). These models varied in three respects: 1) the measure of RHP used (relative group size, focal group size, or adult males; these variables were correlated and thus could not be included in each model simultaneously); 2) the inclusion of an interaction term between certain variables; and 3) the presence or absence of unweaned infants as a predictor (the number of infants was strongly correlated with group size, so I omitted it from the models in which group size was the measure of RHP). Rather than test all possible interaction terms, I chose only a subset relating to food defense because of the large number of variables relating to these hypotheses (Table II). For instance, feeding sites are expected to be defended when overall food abundance is low, feeding site dispersion is high, and the focal group has not yet exploited the patch; thus, I tested an interaction between food abundance–distribution and site occupation time. I created one set of 18 models for females and another set for males, and used the information-theoretic approach to choose among models within a set (Burnham and Anderson 2002). I checked for evidence of multicollinearity among the independent variables by examining variance inflation factors (range:

1.08–1.40) and condition indices (range: 10.32–19.57), all of which were well below recommended thresholds (Tabachnick and Fidell 2007).

I calculated Akaike Information Criterion values (adjusted for small sample sizes, AIC_C) for each model and arranged them by their AIC_C weights (ω_i). The confidence set of best models included those with ω_i scores within 12.5% of the highest ranked model (Burnham and Anderson 2002). To determine the strength of the best model(s) relative to the next-best model, I divided the ω_i score of the former by the ω_i score of the latter (Burnham and Anderson 2002). I then removed all terms with $P > 0.10$ from the best global model(s) to arrive at the final best model, and checked to ensure that this final model had a lower AIC_C value than the version(s) that included the nonsignificant terms.

The random effects were not a significant predictor of variance for any of the models and because they unnecessarily inflate the degrees of freedom, I repeated the entire model selection process using fixed effects-only models; the best models from the selection process with random effects were the same as the models from the process without random effects. I report the results of the fixed effects-only models.

Table II The initial set of multiple regression models, indicating the predictor variables and interactions included in each model, for evaluating responses by grey-cheeked mangabey groups to real and simulated neighbors at the Ngogo site in Kibale National Park, Uganda, from January 2008 through March 2009

Hypothesis:	1	1	1	2, 3	2	4	5, 6	7
Variable:	Food	Feeding	Site	Zone in	Zone in	Unweaned	Estrous	Resource-
Model	abundance– distribution	patch size	occupation time	Zone in focal's range	Zone in caller's range	infants	females	holding potential
1a	•	•	•	•	•	•	•	•R
1b	•	•	•	•	•		•	•F
1c	•	•	•	•	•	•	•	•M
2a	•	•	•	○	•	•	•	○R
2b	•	•	•	○	•		•	○F
2c	•	•	•	○	•	•	•	○M
3a	•	•	•	○	○	•	•	•R
3b	•	•	•	○	○		•	•F
3c	•	•	•	○	○	•	•	•M
4a	○	•	○	•	•	•	•	•R
4b	○	•	○	•	•		•	•F
4c	○	•	○	•	•	•	•	•M
5a	•	○	○	•	•	•	•	•R
5b	•	○	○	•	•		•	•F
5c	•	○	○	•	•	•	•	•M
6a	•	•	○	○	•	•	•	•R
6b	•	•	○	○	•		•	•F
6c	•	•	○	○	•	•	•	•M

“•” indicates a variable included as a main effect; ○ indicates a variable included in the model as a main effect and as part of an interaction with another variable. Resource-holding potential: R = relative group size; F = focal group size; M = number of males.

To more fully evaluate the role of site occupation time on male and female movement responses, I conducted two *post hoc* analyses. First, I compared sex-specific post-call movements to group-wide pre-call movements, and because both parameters were categorical, I used χ^2 tests. If male and female approaches were merely a continuation of group-wide movement before the interaction, then approaches should occur more often when the focal group had been moving toward the neighbor before its call. Second, for IGIs that occurred between two focal groups, I used logistic regressions to compare the occurrence of male and female approaches based on the focal and neighboring groups' site occupation times. Sex-specific binary responses, e.g., males approach or do not approach, were the dependent variables and the focal and opposing groups' site occupation times (short or long) the independent variables.

All statistical tests were two-tailed, with $\alpha = 0.05$, and were performed in Stata v.12 (StataCorp LP, College Station, TX).

Ethical Note

Permissions to conduct this study were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the Uganda Office of the President. Data collection protocols were approved by the Columbia University Institutional Animal Care and Use Committee (AC-AAAA8112), and I conducted all research activities in compliance with Ugandan national laws and the Association for the Study of Animal Behaviour/Animal Behavior Society guidelines for the use of animals in research.

Table III Wilcoxon tests of contextual differences between playback trials and naturally occurring intergroup interactions (IGIs) among grey-cheeked mangabey groups at the Ngogo site in Kibale National Park, Uganda, from January 2008 through March 2009

Hypothesis	Variable	Z	P	Playbacks		IGIs	
				N	Median (IQR)	N	Median (IQR)
1	Overall food abundance	2.33	0.02	71	7 (4–11)	68	4 (3–9)
1	Feeding site distribution	−2.05	0.04	71	1.0 (0.6–1.6)	67	1.5 (0.5–2.5)
1	Food patch size	1.61	0.11	71	7.9 (5.8–10.4)	63	7.1 (4.6–9.9)
1	Site occupation time	3.18	<0.01	71	40 (30–70)	58	20 (0–60)
2, 3	Focal zone	−1.42	0.16	71	50 (50–75)	69	75 (50–75)
2	Neighbor zone	6.60	0.00	71	100 (100–125)	64	75 (50–100)
4	Unweaned infants	−1.60	0.11	71	1 (0–2)	69	2 (1–2)
5, 6	Estrous females	1.33	0.18	71	2 (1–2)	69	1 (1–2)
7	Relative group size	−2.23	0.03	71	−2 (−3–1)	69	0 (−2–2)

Variables with significantly different distributions across PBs and IGIs are indicated in bold. IQR = interquartile range.

Results

Overview of Playbacks and IGIs

I conducted 71 experimental playback trials with six grey-cheeked mangabey focal groups (see ESM). The probability that females or males approached the speaker was not associated with trial order (Wilcoxon test: females: $N_{\text{approach}} = 11$, $N_{\text{stationary}} = 60$, $Z = -0.65$, $P = 0.51$; males: $N_{\text{approach}} = 34$, $N_{\text{stationary}} = 37$, $Z = -0.55$, $P = 0.58$), indicating that subjects did not habituate to the playback setup.

My team and I observed 45 IGIs between focal groups, beginning from the point at which groups were in auditory contact, but not yet in visual contact (see ESM). We recorded information on both the focal and opposing groups during 24 of these IGIs, resulting in 69 group observations. IGIs occurred more frequently in the periphery of the focal group's range (74% of IGIs) than in the core.

In both the IGIs and playbacks, each group within a dyad initiated some interactions (IGIs: a group initiated a mean of $56 \pm \text{SD } 31\%$ of its interactions with a particular

Table IV Information-theoretic comparison of multiple logistic regression models of responses by female and male grey-cheeked mangabeys during pooled playback trials and naturally occurring intergroup interactions at the Ngogo site in Kibale National Park, Uganda, from January 2008 through March 2009

Model	Females						Males					
	LR χ^2	<i>P</i>	df	AIC _c	Δ_i	ω_i	LR χ^2	<i>P</i>	df	AIC _c	Δ_i	ω_i
1a	9.51	0.30	9	134.28	4.27	0.03	15.15	0.06	9	174.88	2.58	0.07
1b	8.80	0.27	8	132.66	2.65	0.07	11.09	0.14	8	176.61	4.31	0.03
1c	7.73	0.46	9	136.06	6.05	0.01	13.33	0.10	9	176.71	4.40	0.03
2a	9.52	0.39	10	136.65	6.63	0.01	15.15	0.09	10	177.25	4.95	0.02
2b	8.81	0.36	9	134.99	4.97	0.02	11.09	0.20	9	178.94	6.64	0.01
2c	7.75	0.56	10	138.42	8.40	0.00	14.20	0.12	10	178.21	5.91	0.01
3a	13.48	0.14	10	132.68	2.67	0.06	15.42	0.08	10	176.98	4.68	0.02
3b	12.99	0.11	9	130.81	0.79	0.17	11.58	0.17	9	178.46	6.16	0.01
3c	11.78	0.23	10	134.38	4.37	0.03	13.74	0.13	10	178.67	6.37	0.01
4a	9.75	0.37	10	136.41	6.40	0.01	16.66	0.05	10	175.75	3.44	0.04
4b	8.98	0.34	9	134.81	4.79	0.02	12.52	0.13	9	177.51	5.21	0.02
4c	7.95	0.54	10	138.22	8.20	0.00	14.91	0.09	10	177.49	5.19	0.02
5a	11.68	0.23	10	134.48	4.47	0.03	20.10	0.02	10	172.30	0.00	0.24
5b	11.09	0.20	9	132.70	2.69	0.06	17.48	0.03	9	172.55	0.25	0.22
5c	10.03	0.35	10	136.13	6.12	0.01	18.69	0.03	10	173.72	1.42	0.12
6a	15.37	0.08	10	130.79	0.78	0.17	17.57	0.04	10	174.84	2.54	0.07
6b	13.78	0.09	9	130.01	0.00	0.25	14.10	0.08	9	175.93	3.63	0.04
6c	13.24	0.15	10	132.93	2.91	0.06	15.73	0.07	10	176.68	4.38	0.03

$N = 123$ group observations for all models. The sets of best candidate models are indicated in bold. See Table II for a list of variables included in each model.

neighbor, $N = 18$ focal–dyad combinations; playbacks: a group approached in $48 \pm \text{SD } 31\%$ of trials in response to a particular neighbor's calls, $N = 15$ focal–dyad combinations), indicating that call-and-response sequences were variable. Compared to IGIs, the playbacks tended to pit the focal group against larger neighbors and occurred in more peripheral areas of the neighboring group's range, and when the focal group had been in the interaction site for >30 min (Table III). Playbacks also occurred under different conditions of food availability compared to IGIs, i.e., during periods of higher overall food abundance and when feeding sites were randomly distributed.

Sex-Specific Responses

During playbacks and IGIs, the most common response by females was to remain within the body of the group and to approach at low frequencies (playbacks = 15% of trials, IGIs = 26% of interactions); they approached the simulated or real neighbor only if males also approached. Males approached neighbors approximately as often as they remained stationary (approaches during playbacks = 48%, IGIs = 52%). The frequencies of female and male approach and stationary responses to experimental trials and IGIs were not significantly different (females: Pearson $\chi^2_1 = 2.39$, $P = 0.12$; males: $\chi^2_1 = 0.26$, $P = 0.61$), indicating that groups responded to simulated intruders in much the same way as to real intruders.

Among the initial set of female models (Table IV), there was one best-candidate model of female movement responses; this model explained 47% more variation than the next best model. Females were most likely to approach a real or simulated neighboring group when the focal group had recently arrived in the interaction location (Table V). In addition, when the focal group had been in the interaction location for >30 min, females were slightly more likely to approach the neighbor if the interaction occurred in

Table V The best models of approach responses by female and male grey-cheeked mangabeys at the Ngogo site in Kibale National Park, Uganda, in pooled playback trials and intergroup interactions from January 2008 through March 2009

Sex	Variables	Coefficient	Odds	SE	95 % CI	<i>P</i>
Females ($N = 123$ observations, $\text{df} = 4$, $\text{LR } \chi^2 = 11.94$, $P < 0.01$, $\text{AIC}_C = 120.60$)						
	Focal group zone	0.21	1.23	0.12	−0.02 0.43	0.08
	Site occupation time	1.01	2.74	1.00	−0.96 2.97	0.32
	Interaction (site occupation $\times$ focal zone)	−0.44	0.64	0.19	−0.82 −0.06	0.02
	Intercept	−1.86	0.16	0.66	−3.15 −0.56	0.01
Males ($N = 123$ observations, $\text{df} = 6$, $\text{LR } \chi^2 = 17.17$, $P < 0.01$, $\text{AIC}_C = 165.99$)						
	Focal group zone	0.14	1.15	0.08	−0.01 0.30	0.07
	Neighboring group zone	0.15	1.16	0.08	−0.01 0.30	0.06
	Site occupation time	−2.68	0.07	0.91	−4.46 −0.90	0.00
	Feeding patch size	0.02	1.02	0.04	−0.07 0.10	0.72
	Interaction (site occupation $\times$ patch size)	0.24	1.28	0.10	0.04 0.45	0.02
	Intercept	−0.69	0.50	0.71	−2.08 0.71	0.34

Significant covariates are indicated in bold.

Fig. 1 Percentage of interactions in which grey-cheeked mangabey (a) females and (b) males at the Ngogo site in Kibale National Park, Uganda, approached the opposing group from January 2008 through March 2009. Overall, females and males approached in 20% and 51% of interactions. Focal zone: core = inner 50 % minimum convex polygon; periphery = outer 45% minimum convex polygon. Site occupation time: short = ≤ 30 min; long = > 30 min. Patch size: small = the lowest quartile of patch sizes; medium = the middle two quartiles of patch size; large = the highest quartile of patch size.

the periphery than in the core of the focal group's range (Fig. 1a). Though females initiated close-range interactions only if males were also participating, male participation could not be included as a predictor because it prevented the models from reaching convergence.

There were two best-candidate models of male responses among the initial set of global models (Table IV); the best model explained only 13% more variation than the second best model, but the latter explained 80% more variation than the third-ranked model. After the nonsignificant terms were removed from these two models, they were identical, yielding one final model of male approach responses that contained a main effect of site occupation time; males approached a neighboring group more often if the focal group had recently arrived at the interaction location (Table V). There was also an interaction between site occupation time and feeding patch size (Table V), suggesting that small and large patches were depleted quickly and slowly, respectively, which

corresponded with a low frequency of male approaches in small, already depleted patches and a high frequency of approach in large, not-yet-depleted patches (Fig. 1b).

Site occupation time was a significant predictor for both males and females, so I conducted two *post hoc* analyses to investigate the significance of this predictor further. First, I tested whether approaches were merely a continuation of prior movement by comparing male and female approach responses to preinteraction group travel (categorized as toward, stationary, or away from the neighbor or speaker, based on the distance between the focal and caller). Sex-specific responses were not a continuation of group movement (females, Pearson $\chi^2_2 = 1.19$, $P = 0.55$; males, $\chi^2_2 = 2.81$, $P = 0.25$). Second, I investigated whether approach responses were affected simultaneously by the focal and neighboring groups' site occupation times. Both sexes were most likely to approach a neighboring group when there was an asymmetry in occupation time, such that the focal group had recently arrived and the neighboring group had been in the interaction location for a long period (Fig. 2; logistic regression: females, $N = 36$ group-IGIs, LR $\chi^2_2 = 6.40$, $P = 0.04$; males, LR $\chi^2_2 = 7.07$, $P = 0.03$).

Discussion

In response to vocalizations from real and simulated neighboring groups, grey-cheeked mangabeys in a high-density population initiated contests over food patches. More specifically, they were most likely to approach neighboring groups to gain or maintain access to feeding sites that they had recently entered, and presumably not yet fully exploited (supporting Hypothesis 1). There was no evidence that either sex attempted to maintain exclusive access to the core of the home range (contradicting Hypothesis 2), prevent trespassing into the home range (contradicting Hypothesis 3), or prevent food-related intergroup infanticide (contradicting Hypothesis 4). Males did not appear to

Fig. 2 The frequency of approach responses by female and male grey-cheeked mangabeys at the Ngogo site in Kibale National Park, Uganda, as a function of site occupation times during 18 intergroup interactions (IGIs) from January 2008 through March 2009 for which we collected data on both interacting groups (yielding 36 records). Short refers to a site occupation time ≤ 30 min; long is an occupation time > 30 min. Of the 11 IGIs with asymmetrical occupation times, 8 IGIs (73%) were initiated by the newly arrived group, 2 IGIs (18%) by the group that was in the interaction location for > 30 min, and 1 IGI (9%) by both groups simultaneously.

defend female mates (contradicting Hypotheses 5 and 6), and neither male nor female approaches indicated an effect of group RHP (contradicting Hypothesis 7).

Relative to patterns of aggressive escalation and outcomes, contest initiations are rarely examined (*cf.* Putland and Goldizen 1998; Wilson *et al.* 2012). Among Tasmanian native hens (*Gallinula mortierii*), groups with high-quality home ranges are more likely to both initiate and win contests than groups with low-quality ranges (Putland and Goldizen 1998). Among chimpanzees (*Pan troglodytes*), larger parties of males are more likely to initiate and aggressively escalate than smaller parties (Wilson *et al.* 2012). Thus, in these species, it appears that the factors that affect contest initiation also affect other contest phases. Grey-cheeked mangabey behavior only partially adheres to this pattern. Contest initiation and aggressive escalation by male mangabeys indicated defense of feeding sites (rather than defense of core or peripheral home range areas), but whereas patch size predicted male approaches, it did not predict male aggressiveness (Brown 2013). For females, approaches were indicative of feeding site defense, but aggressiveness did not correspond with any known food-related variables. Further analyses are forthcoming to determine whether other contest phases are affected by asymmetries in group size or by the presence of estrous females and vulnerable infants.

Expected Payoffs and RHP

This study is the first to demonstrate the importance of temporary site residency, specifically with regard to the initiation of intergroup contests. Though residency is known to affect contests in some social and asocial species, its effects have been measured only in terms of later contest phases, e.g., display duration and outcome, and the expected benefits are thought to increase with residency duration (Kemp and Wiklund 2004; Stevens 1988; Takeuchi and Honda 2009). Here, residency is evaluated specifically for isolated resources and the expected benefits are assumed to decrease over time, because the longer a group spent in a particular feeding site, the more likely they should be to have reached their giving-up density for that resource (Prediction 1b; Brown 1988; Houle *et al.* 2006). Male and female mangabey responses fit this prediction: the likelihood of approach decreased as residence time increased. Though a more explicit analysis is needed to test the hypothesis that increasing residency time yields decreasing payoffs, these results indicate the importance of site residency, which does not appear to have been evaluated in previous studies of primate intergroup contests.

Unlike other group-living species (spotted hyena, *Crocuta crocuta*: Benson-Amram *et al.* 2011; domestic dog, *Canis familiaris*: Bonanni *et al.* 2011; white-faced capuchin, *Cebus capucinus*: Crofoot *et al.* 2008; banded mongoose, *Mungos mungo*: Furrer *et al.* 2011; black howler monkey, *Alouatta pigra*: Kitchen 2003; lion, *Panthera leo*: McComb *et al.* 1994; chimpanzees, *Pan troglodytes*: Wilson *et al.* 2012), there was no evidence that relative, absolute, or male group size affected patterns of approach. The lack of a group size effect is not unique, but is usually observed in species that defend explicit boundaries in the periphery of the home range (Bornean gibbon, *Hylobates muelleri*: Mitani 1985; ringtailed lemur, *Lemur catta*: Pride *et al.* 2006; Tasmanian native hen, *Gallinula mortierii*: Putland and Goldizen 1998). Grey-cheeked mangabeys do not aggressively defend the home range periphery (Brown 2013), so the absence of a group size effect is somewhat surprising. It is possible that, for mangabeys, group size is

not an adequate measure of RHP; male mangabeys participate in all aggressive IGIs and are the primary participants, so perhaps the size, strength, or aggressiveness of group males is a better determinant of RHP than the number of participants (Batchelor and Briffa 2010). Alternatively, the number of actual participants may represent RHP more accurately than the number of potential participants (Zhao and Tan 2010), or RHP may only be influential in determining other contest aspects (duration, intensity, or outcome). Further exploration is needed to test these possibilities, and more broadly, a theoretical framework is needed to explain why species vary in the relative importance of RHP and payoff asymmetries across contest phases.

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