

# Vocal and movement responses of mantled howler monkeys (*Alouatta palliata*) to natural loud calls from neighbors

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## Abstract

Loud calls (i.e., long-range acoustic signals) regulate resource competition among neighboring groups of conspecifics in several nonhuman primate species. Ultimate explanations for primate loud calls include mate, offspring, and food defense. Additionally, loud calls may provide valuable information pertaining to the identity and health status of callers, their competitive abilities, and their spatial location. The loud calls of howler monkeys (*Alouatta*) have been thoroughly studied and seem to play an important function in the defense of valuable resources in a variety of socioecological contexts. Here, we examined whether the behavioral responses of mantled howler monkeys (*Alouatta palliata*) to natural loud calls from neighbors are linked to three factors: food availability, familiarity, and distance between groups. We studied three groups of mantled howler monkeys at La Flor de Catemaco (Los Tuxtlas, Mexico) for 15 months (1817 observation hours), during which we recorded 236 neighbor loud calls. Food availability per se did not influence the behavior of groups receiving loud calls, although males produced longer vocal responses toward unfamiliar neighbors when food availability decreased. Groups vocalized quicker and both vocalized and moved for longer after loud calls from unfamiliar neighbors. Additionally, groups vocalized and moved for longer at shorter distances from unfamiliar neighbors compared with familiar neighbors. Finally, groups usually moved away from calling neighbors that were closer. These results indicate that the behavioral responses of mantled howler monkeys to loud calls from neighbor groups are associated with the integration of information pertaining to caller identity as well as to their ecological and spatial context.

## KEYWORDS

advertisement of occupancy, familiarity, intergroup spacing, movement, vocalizations

## 1 | INTRODUCTION

Empirical evidence suggests that the motivation to engage in aggressive intergroup encounters is based on the value of the reward in relation to the cost of the fight (Parker, 1974; Parker & Rubenstein, 1981). Individuals living in groups will incur the costs of

fighting only to defend or acquire significantly limited resources (Enquist & Leimar, 1987, 1990). Otherwise, they are expected to avoid contact with opponents, preventing the high costs of aggressive encounters and reducing intergroup feeding and mating competition (Kelly, 2005; Kitchen & Beehner, 2007; Wrangham et al., 2007).

Loud calls (i.e., long-range acoustic signals) regulate resource competition among neighboring groups of conspecifics in several nonhuman primate species as well as in other mammals (Delgado, 2006; Leighty et al., 2008; Mitani & Stuht, 1998; Owen-Smith, 1975; Wich & Nunn, 2002). Ultimate explanations for primate loud calls include mate (e.g., Kitchen, Cheney, et al., 2004; Steenbeek & Assink, 1998; Wich & Nunn, 2002), offspring (e.g., Kitchen, Horwich, et al., 2004; Steenbeek et al., 1999; Wich et al., 2002), and food (e.g., Fashing, 2001; Harris, 2006) defense. Loud calls may provide valuable information pertaining to the identity and health status of the actors, their competitive abilities, and their spatial localization (Erb et al., 2013; Fischer et al., 2004; Kitchen, 2004; Wich et al., 2002). Therefore, loud calls can regulate the spatial distribution of neighboring groups, via signals that result in an increase, maintenance, or decrease of the distance between groups, thus affecting the frequency of intergroup encounters (Brown & Waser, 2018).

All *Alouatta* males produce potent low-frequency loud calls that can be heard over a kilometer in dense tropical forests (Whitehead, 1995). Loud calls are produced periodically during the day by one or more males of the group (Horwich & Gebhard, 1983; Schön, 1986). There is abundant evidence that howler monkey loud calls are important for intergroup communication and for regulating the use of space between neighboring groups (e.g., Ceccarelli et al., 2019; Chiarello, 1995; da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Drubbel & Gautier, 1993). For instance, black howler monkeys (*Alouatta pigra*) and mantled howler monkeys (*Alouatta palliata*) are more likely to approach a calling group when food availability decreases (Hopkins, 2013; Van Belle & Estrada, 2019), and the latter are more likely to approach and howl toward simulated intruders located in resource-rich areas (Whitehead, 1989). This is consistent with evidence that howler monkey loud calls are not randomly produced across home ranges (e.g., da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Horwich & Gebhard, 1983; but see Holzmann et al., 2012).

Movement responses of mantled howler monkeys—but not of black howler monkeys (Van Belle & Estrada, 2019)—to loud calls are also influenced by intergroup dominance relationships, with subordinates approaching dominants as a possible strategy to queue for access to productive food sources (Hopkins, 2013). In black howler monkeys, the likelihood to howl toward and approach simulated loud calls increases in alpha males facing favorable numeric odds (i.e., the number of male callers relative to the number of male listeners: Kitchen, 2004), when small offspring are present (Kitchen, 2004), and in groups receiving loud calls from incongruent locations (i.e., a loud call from a known neighbor played back from a location outside its home range: Briseño-Jaramillo et al., 2015). Black howler monkeys approach calling neighbors more frequently than expected by chance at closer distances (Van Belle & Estrada, 2019), although the distance between groups does not affect mantled howler monkey responses to loud calls (Hopkins, 2013).

The loud calls of howler monkey males seem, therefore, to be functionally linked to the access and defense of food sources as well as to the defense of vulnerable infants. Less is known about the possible role of loud calls in mate defense (Holzmann et al., 2012; Sekulic, 1982),

although the compelling evidence for strong intrasexual male competition (e.g., Cristóbal-Azkarate et al., 2004, 2007; Rangel-Negrín et al., 2011) suggests that loud calls may have also evolved under such selective pressure (Kitchen et al., 2015). Thus, the loud calls of male howler monkeys may ultimately serve to defend valuable resources and are proximately linked to several contexts, including the identity and status of calling individuals, group size and composition, group location, and food availability (da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Holzmann et al., 2012; Kitchen, 2004; Kitchen, Cheney, et al., 2004; Kitchen, Horwich, et al., 2004; Van Belle & Estrada, 2019; Van Belle et al., 2013; Van Belle & Scarry, 2015; Whitehead, 1989).

Here, we studied the behavioral responses of mantled howler monkeys to naturally occurring loud calls. Movement in response to loud calls is a straightforward indicator of the consequences of vocal communication for intergroup spatial organization (e.g., Waser, 1976, 1977). Still, vocal reciprocation (i.e., loud calls eliciting loud calls) may allow for the spatial regulation of neighboring groups, even in the absence of immediate movement responses (e.g., Fan et al., 2009). Thus, we assessed both the vocal and movement responses of mantled howler monkeys to neighbor loud calls. We tested the hypothesis that behavioral responses to neighbor loud calls are linked to a food defense function (Hopkins, 2013; Van Belle & Estrada, 2019). Given that males from some howler monkey populations loud call more when food availability decreases (Chiarello, 1995; Drubbel & Gautier, 1993; Van Belle et al., 2014) and that at high food availability groups may be more willing to move away from opponents to avoid the costs of aggressive encounters (Harrison, 1983; Hopkins, 2013), we predicted that, as food availability decreases vocal and movement responses should be quicker and longer, and groups should move toward calling neighbors.

However, intergroup encounters are risky (e.g., may entail physical injury: Garber & Kowalewski, 2011) and mutual avoidance between groups is a predicted outcome of repeated interactions between conspecifics (Maynard-Smith, 1974; Maynard-Smith & Parker, 1976). Accordingly, there is ample evidence that groups tend to respond less aggressively to intrusions from familiar neighbors than to unfamiliar intruders, which has been described as a “dear enemy effect” (Cheney et al., 1996; Ydenberg et al., 1988). Thus, we also hypothesized that behavioral responses to loud calls should be affected by familiarity and predicted that, independently of variation in food availability, the responses to loud calls from unfamiliar neighbors should be stronger (i.e., quicker, longer, and groups approaching calling neighbors) than to calls from familiar neighbors. Finally, as the likelihood of intergroup encounters should increase at closer distances, we hypothesized that the behavioral responses of groups should be conditional on the distance between calling and receiving groups. Thus, groups receiving loud calls should vocalize quicker and move for longer as well as retreat from their position at shorter distances to avoid the costs of aggressive encounters (Clutton-Brock & Albon, 1979; Clutton-Brock et al., 1979). Nevertheless, the direction of the movement should depend on food availability and familiarity with the caller: When food availability is low and calling groups are unfamiliar, receiving groups should approach, even at short intergroup distances.

## 2 | METHODS

### 2.1 | Ethical note

Our study complied with the ASP Code of Best Practices in Field Primatology and to the ASP Principles for Ethical Treatment of Non-Human Primates. No animals were captured or handled during this study. Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/10637/11 and SGPA/DGVS/04999/14) and followed the legal requirements of Mexican law (NOM-059-SEMARNAT-2010).

### 2.2 | Study site and subjects

We conducted our study in a forest fragment with ca. 100 ha located at La Flor de Catemaco (18°26'43"N, 95°02'49"W; Los Tuxtlas, Veracruz, Mexico). The vegetation in this fragment is mainly tall evergreen tropical forest. Food availability to howler monkeys shows small seasonal variation and is higher at La Flor de Catemaco than in other sites (Cano-Huertes et al., 2017). The nearest forest fragment occupied by mantled howler monkeys is ca. 1 km, across a pastureland.

Data were collected between January 2016 and March 2017. By the end of this study, 24 individuals inhabited the fragment, 20 of them divided into three groups lived in groups, and four living solitarily. We focused on the three groups: G1, with three adult females, three adult males and one infant; G2, comprising four adult females, three adult males, and three infants; G3, including two adult females and one adult male. Groups G1 and G2 included lactating infants with less than 12 months of age throughout the study. G1 and G2 have co-resided at La Flor de Catemaco since 2005, whereas G3 was first observed at the site by the end of 2014, comprising two adult females and one adult male. Throughout 2015, G3 had strong intergroup encounters with resident groups that involved prolonged loud calling bouts as well as displays and chases between G1 and G3 males. On August 20, 2015, one of G3 females gave birth to an infant that died one month later, and the mother transferred to G1 by May 2016. By July 2016, a new female immigrated to G3, which again comprised two adult females and one adult male. Thus, our study groups may be classified as long-term (G1 and G2) and short-term (G3) residents and thus dyadic familiarity relationships classified as familiar (G1–G2) or unfamiliar (G1–G3, G2–G3).

### 2.3 | Behavioral data collection

All subjects were fully habituated to the presence of researchers (i.e., they paid no attention to us and our presence did not interfere with their behavior) and were easily identified by anatomical and physiognomic traits. We conducted observations four days per week between 6:00 a.m. and 6:00 p.m., for a total of 127 days. Each day two observers (E. C. and A. C.-F.), followed a

**TABLE 1** Sampling effort and number of recorded behavioral events analyzed in this study

Group	Sampling hours	No. of neighbor loud calls	No. of vocal responses	No. of movement responses
G1	886	94	60	22
G2	826	77	36	14
G3	105	65	53	22
Total	1817	236	149	58

different study group simultaneously (focal groups). We recorded loud calls produced by the focal groups using all-occurrences sampling (Altmann, 1974), for a total of 1817 h (Table 1). We considered two consecutive vocalizations to be independent when they were at least 10 min apart ( $N = 236$  events; Hopkins, 2013). We recorded the vocal and movement responses of the focal group receiving loud calls from another focal group. We defined a vocal response as a loud call produced within 60 min of the initial loud call (Kitchen, 2004; Kitchen et al., 2018). One hundred and forty-nine vocal responses occurred within this period whereas 87 occurred 60 min after the loud call. We assessed vocal responses via their latency, defined as the time between the original loud call and the first vocal response, and duration, defined as the sum of time spent loud calling by the recipient group within 60 min of the initial loud call. We defined a movement response as any occasion in which the group receiving loud calls started traveling within the first 60 min of the initial loud call ( $N = 159$ ). We excluded events in which groups were traveling when receiving a loud call. As we could only measure the distance between two groups, we also excluded events in which two neighboring groups loud called simultaneously. Fifty-eight movement responses adhered to our definition whereas 103 occurred after the 60-min period. As with vocal responses, we studied movement responses using the latency to the first movement and the duration of all movements recorded within the 60-min post-loud call period.

We marked and located with a global positioning system all trees occupied by focal groups. We used QGIS 3.10 (QGIS Development Team, 2014) to determine the geographic position and the Euclidian distance between focal groups when a loud call was produced. With this geolocation information, we further classified movement responses as approaches, if they were less than  $\pm 90^\circ$  from the line connecting the position of the calling group and the original position of the group receiving the loud call ( $N = 26$ ), or retreats if they were more than  $\pm 90^\circ$  ( $N = 18$ ; Hopkins, 2013).

### 2.4 | Determination of food availability

We assessed food availability through the estimation of the density, distribution, and abundance of fruits and leaves, which are the main

food items in mantled howler monkey diets (Dias & Rangel-Negrín, 2015). Within the home ranges of each study group, we plotted 10 linear transects of  $50 \times 2$  m (i.e.,  $1000 \text{ m}^2$ ) in which we identified all trees at the species level with a diameter at breast height (DBH)  $\geq 10$  cm (Gentry, 1982). We identified 128 trees from 17 different species that belonged to the top food species, that is, those that contribute 80% of the feeding time, previously reported for mantled howler monkeys in Los Tuxtlas (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007). To assess temporal changes in the presence of fruits and leaves, we marked all identified transect trees and once a week we noted the abundance of plant items with semiquantitative scores (Fournier, 1978): 0 = total absence; 0.25 = presence in 0%–25% of the total coverage of the frond of the tree; 0.50 = 26%–50%; 0.75 = 51%–75%; and 1 = 76%–100%. We calculated mean weekly fruit biomass per tree as  $\text{fruit biomass} = \text{mean monthly Fournier score} \times (47 \times \text{DBH}^{1.9})$ , where  $47 \times \text{DBH}^{1.9}$  expresses an allometric relationship between trunk size and fruit production (Whittaker & Woodwell, 1968). We calculated mean weekly mature and young leaf biomass per tree as  $\text{leaf biomass} = \text{mean monthly Fournier score} \times (38.4 \times \text{DBH}^{1.65})$ , where  $38.4 \times \text{DBH}^{1.65}$  expresses an allometric relationship between trunk size and leaf production (Niklas, 1994).

We also calculated the importance index of each top food species in the home range of each group as a measure of its availability. We first calculated the density (number of trees per species/ $1000 \text{ m}^2$ ), frequency (number of transects in which the species was found/10 transects), and dominance (sum of basal area of the species in the sampled  $1000 \text{ m}^2$ ) of each species. We then converted these measures to percentages by dividing each species' value by the sum of values across all species and multiplying that result by 100. We calculated the importance index of each species as the sum of its relative density, frequency, and dominance, and calculated weekly fruit and leaf availability by first multiplying weekly mean fruit and leaf biomass per species by its importance index (Agostini et al., 2010), and then summing these values across of all species per plant part. We calculated weekly total food availability as the sum fruit and leaf availability per week.

Food availability measures were highly correlated in our data set (total and fruit availability  $r = 0.97$ ,  $p < 0.001$ ; total and leaf availability  $r = 0.91$ ,  $p < 0.001$ ; fruit and leaf availability  $r = 0.81$ ,  $p < 0.001$ ; Figure 1a). To avoid collinearity and facilitate the interpretation of the results pertaining to interaction terms in the models described below, we used cluster analysis to categorize food availability throughout the study. We first determined the optimal number of clusters to use with the silhouette method (De Amorim & Hennig, 2015), which indicated that we should define two clusters (Figure 1b). We then used *k*-means clustering to classify study months as high/low in terms of food availability. The resulting clusters had within-cluster sum of squares of 4.2 (Cluster 1) and 2.8 (Cluster 2). According to this analysis, the months of May to September were high-availability months whereas October to April were low-availability months.

## 2.5 | Data analysis

We only analyzed cases where receiver groups responded within 60 min of a neighbor loud call. We tested our predictions with linear mixed models (LMM) and generalized linear mixed models (GLMM) in R package "lme4." We ran five models, one for each dependent variable: latency to vocal responses (LMM); duration of vocal responses (LMM); latency to movement responses (LMM); duration of movement responses (LMM); direction of movement (approach/re-treat, binomial GLMM). We log-transformed all dependent variables in LMMs to achieve normal distribution and checked that the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting Q-Q plots and the residuals plotted against the fitted values for each model. Model residuals did not deviate significantly from normality (Kolmogorov–Smirnov tests;  $p > 0.05$ ). In all models, fixed predictors were (i) food availability in the month in which each loud call event was recorded (i.e., high/low); (ii) the distance separating the two groups during a loud call (in m); (iii) familiarity with the calling group (i.e., familiar/unfamiliar); and (iv) two-way interactions between all predictors. In all models, we used the month in which observations were conducted as a random factor to account for the repeated sampling of groups. We considered a predictor to influence a response variable when (i) its estimate's 95% confidence interval did not include zero, and (ii) it had a significance level of  $p < 0.05$ . We examined the influence of the random factor in all models by comparing each of the models described above (complete models) with a null model including only each dependent variable and the random factor with likelihood ratio tests (LRT; function 'anova' from R Package 'car'). All analyses were performed with R 3.6.3 (R Core Team, 2020).

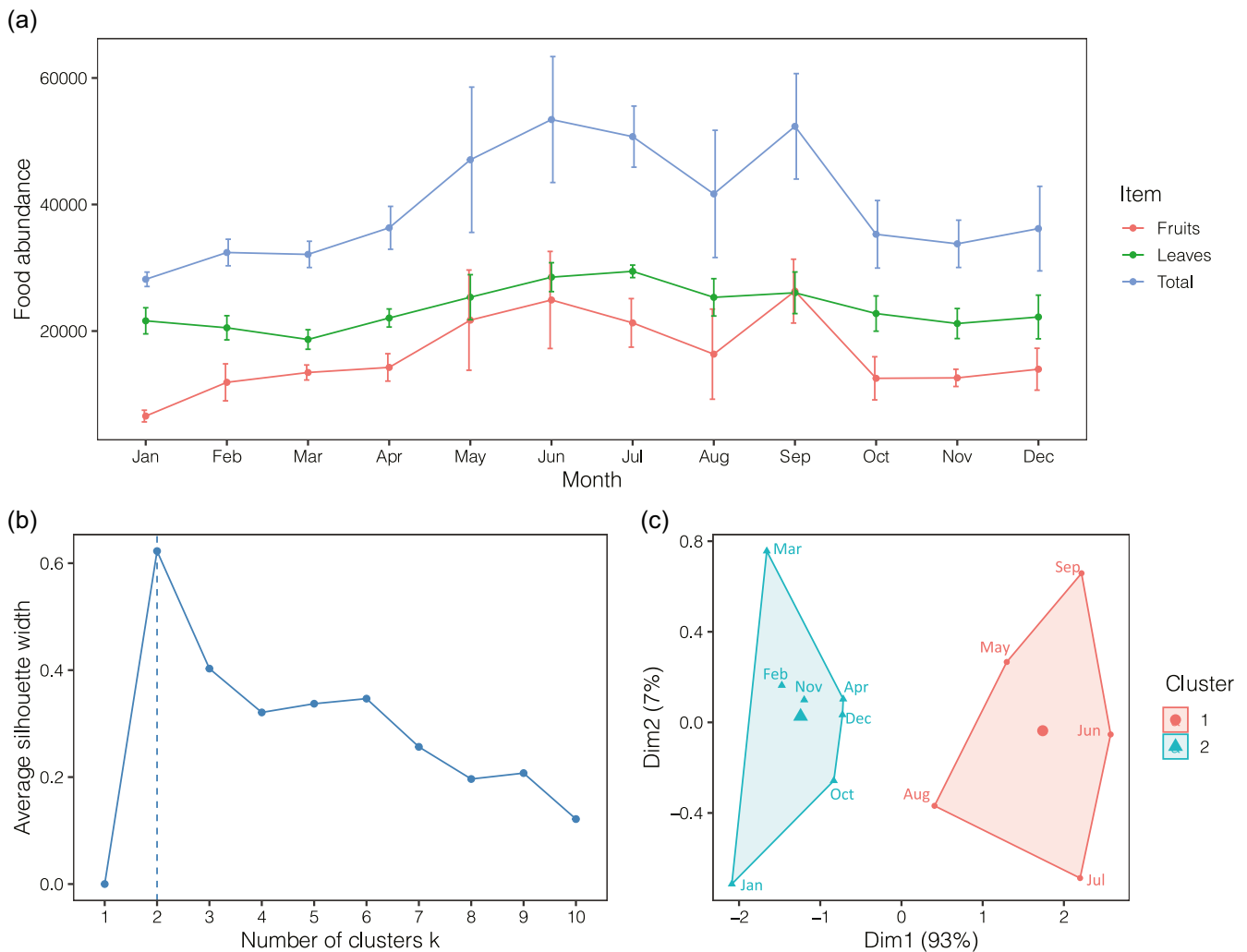
## 3 | RESULTS

### 3.1 | Vocal responses to a calling neighbor

Latency to the first vocal response to a calling neighbor was influenced by familiarity with the caller, such that groups vocalized quicker to the calls of unfamiliar than to those of familiar neighbors (Table 2 and Figure 2a). Concerning the duration of vocal responses, groups vocalized for longer: when received calls from unfamiliar neighbors (Figure 2b); at decreasing distance from the calling group (Figure 2c); at decreasing food availability and received calls from unfamiliar neighbors (Figure 2d); and when received loud calls from unfamiliar neighbors at decreasing distances (Figure 2e).

### 3.2 | Movement responses to a calling neighbor

The complete model for variation in the latency to movement responses was not different from the null model. Groups moved for longer following loud calls from unfamiliar than familiar neighbors (Figure 3a) and when loud calls were produced at decreasing



**FIGURE 1** Classification procedure of food availability for mantled howler monkeys studied at La Flor de Catemaco (Mexico) between January 2016 and March 2017: (a) monthly mean  $\pm$  SD food availability; (b) determination of the optimal number of clusters to be defined in a cluster analysis using the silhouette method; (c) clusters that were defined with a *k*-means cluster analysis

distances by unfamiliar neighbors (Figure 3b). Concerning the direction of movement, only the distance between groups determined the direction of movement, with an increased likelihood of moving away from calling neighbors at decreasing distances (Figure 3c).

## 4 | DISCUSSION

We examined the vocal and movement responses of mantled howler monkeys to loud calls produced by neighbors in relation to three factors: food availability, familiarity, and distance. Contrary to the first prediction, food availability per se did not influence the behavior of groups receiving loud calls, although males produced longer vocal responses to unfamiliar neighbors when food availability decreased. Concurring with the second prediction, familiarity affected the latency and duration of vocal responses as well as the duration of movement responses: groups vocalized quicker and both vocalized and moved for longer after loud calls from unfamiliar neighbors.

Additionally, groups vocalized and moved for longer at decreasing distances from unfamiliar neighbors compared with familiar neighbors. Finally, groups usually moved away from calling neighbors that were closer, a result that opposes the third prediction. Overall, our results converge with previous evidence that the responses of howler monkeys (reviewed in Kitchen et al., 2015) and other primates (e.g., Benítez et al., 2017; Quattara et al., 2009; Wich et al., 2001) to conspecific loud calls are complex (Cheney & Seyfarth, 2003), and are associated with the integration of contextual information (Seyfarth & Cheney, 2017).

Our study indicates that mantled howler monkeys have strong behavioral responses to loud calls from neighbors with whom they are less familiar. Stronger behavioral responses toward strangers than toward familiar neighbors have been observed in a variety of species, a so-called “dear enemy” effect (Temeles, 1994; Ydenberg et al., 1988). Under a “dear enemy” strategy, mutual knowledge of fighting ability prevents the escalation of unnecessary conflicts (e.g., Thompson et al., 2012;

**TABLE 2** LMM and GLMM results of variation in vocal and movement responses of mantled howler monkeys to neighbor loud calls according to food availability, familiarity with the caller, and the distance separating groups

Model/term	$\beta$	SE	95% CI		t, z <sup>a</sup>	p
			Lower	Upper		
Latency to vocal response (0.26) $\chi^2 = 31.1$ ; $p < 0.001^b$						
Food availability	-0.48	0.98	-2.367	1.406	-0.49	0.624
<b>Familiarity</b>	<b>-3.89</b>	<b>1.38</b>	<b>-4.545</b>	<b>-0.774</b>	<b>-1.37</b>	<b>0.017</b>
Distance	-0.03	0.23	-0.469	0.404	-0.14	0.886
Food availability $\times$ Familiarity	0.29	0.53	-0.726	1.312	0.55	0.580
Food availability $\times$ Distance	0.14	0.16	-0.169	0.441	0.86	0.392
Familiarity $\times$ Distance	0.07	0.24	-0.398	0.545	0.30	0.764
Duration of vocal response (0.30) $\chi^2 = 47.8$ ; $p < 0.001$						
Food availability	0.09	0.51	-0.884	1.064	0.18	0.859
<b>Familiarity</b>	<b>1.61</b>	<b>0.71</b>	<b>0.236</b>	<b>2.982</b>	<b>2.26</b>	<b>0.025</b>
<b>Distance</b>	<b>0.28</b>	<b>0.12</b>	<b>0.056</b>	<b>0.507</b>	<b>2.40</b>	<b>0.018</b>
<b>Food availability <math>\times</math> Familiarity</b>	<b>0.78</b>	<b>0.27</b>	<b>0.252</b>	<b>1.305</b>	<b>2.85</b>	<b>0.005</b>
Food availability $\times$ Distance	-0.09	0.08	-0.245	0.071	-1.06	0.289
<b>Familiarity <math>\times</math> Distance</b>	<b>-0.26</b>	<b>0.13</b>	<b>-0.507</b>	<b>-0.020</b>	<b>-2.08</b>	<b>0.039</b>
Latency to movement response (0.06) $\chi^2 = 4.2$ ; $p = 0.654$						
Food availability	-0.38	1.22	-0.312	0.756	-2.65	1.89
Familiarity	0.44	1.86	0.235	0.815	-3.04	3.92
Distance	0.09	0.32	0.294	0.770	-0.50	0.69
Food availability $\times$ Familiarity	0.29	0.68	0.423	0.674	-0.98	1.56
Food availability $\times$ Distance	0.11	0.20	0.560	0.578	-0.26	0.48
Familiarity $\times$ Distance	-0.19	0.34	-0.557	0.580	-0.82	0.44
Duration of movement response (0.22) $\chi^2 = 16.1$ ; $p = 0.013$						
Food availability	-0.01	0.95	-1.774	1.762	-0.01	0.995
<b>Familiarity</b>	<b>2.96</b>	<b>1.45</b>	<b>0.253</b>	<b>5.669</b>	<b>2.05</b>	<b>0.046</b>
Distance	0.43	0.25	-0.028	0.894	1.76	0.085
Food availability $\times$ Familiarity	-0.02	0.53	-1.004	0.970	-0.03	0.975
Food availability $\times$ Distance	-0.13	0.15	-0.415	0.163	-0.81	0.420
<b>Familiarity <math>\times</math> Distance</b>	<b>-0.54</b>	<b>0.26</b>	<b>-1.030</b>	<b>-0.049</b>	<b>-2.06</b>	<b>0.045</b>
Direction of movement response (0.67) $\chi^2 = 28.3$ ; $p < 0.001$						
Food availability	5.36	5.72	-3.736	20.981	0.94	0.349
Familiarity	5.42	8.14	-10.445	23.964	0.67	0.505
<b>Distance</b>	<b>2.62</b>	<b>1.38</b>	<b>0.457</b>	<b>6.036</b>	<b>1.90</b>	<b>0.058</b>
Food availability $\times$ Familiarity	-0.06	2.01	-4.491	3.753	-0.03	0.977
Food availability $\times$ Distance	-0.79	1.00	-3.538	0.770	-0.80	0.426
Familiarity $\times$ Distance	-1.28	1.57	-4.907	1.502	-0.82	0.415

Note: Significant terms are marked in bold. Values in parenthesis are the pseudo-coefficients of determination of models.

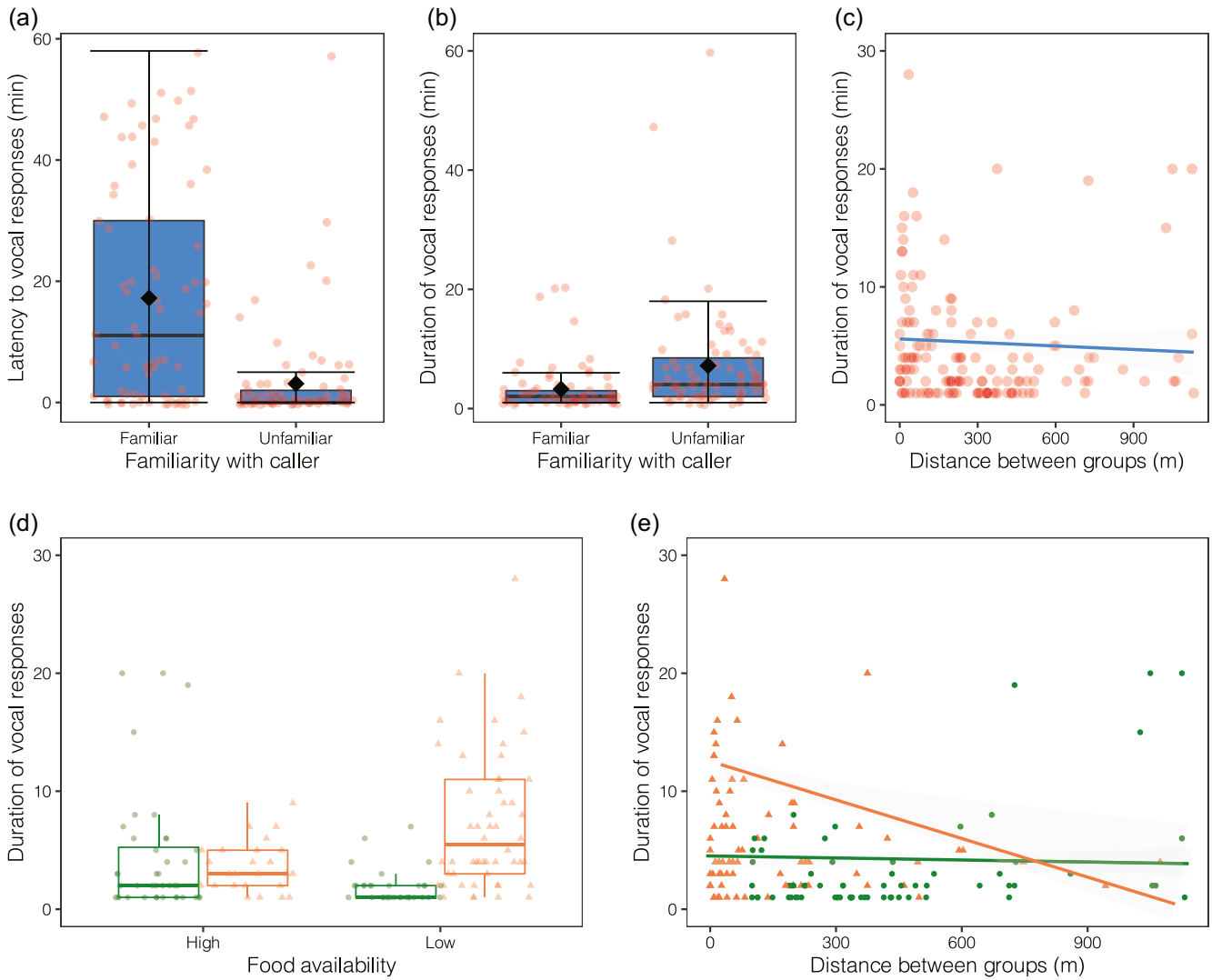
Abbreviations: CI, confidence interval; GLMM, generalized linear mixed model; LMM, linear mixed model.

<sup>a</sup>Statistic is t for linear mixed models and z for generalized linear mixed models.

<sup>b</sup>Results for the complete versus null model comparisons with likelihood ratio tests.

Wich et al., 2002). Additionally, adjacent groups may contain close relatives, which may explain reduced aggression/competition between long-term neighbors (e.g., Reichard & Sommer, 1997). In contrast, unfamiliar individuals represent a

threat as they compete for food resources and mates, may try to take over groups, or commit infanticide (Steenbeek, 1999; Temeles, 1994). Thus, in the context of interactions between unfamiliar neighbors, behavioral responses such as those



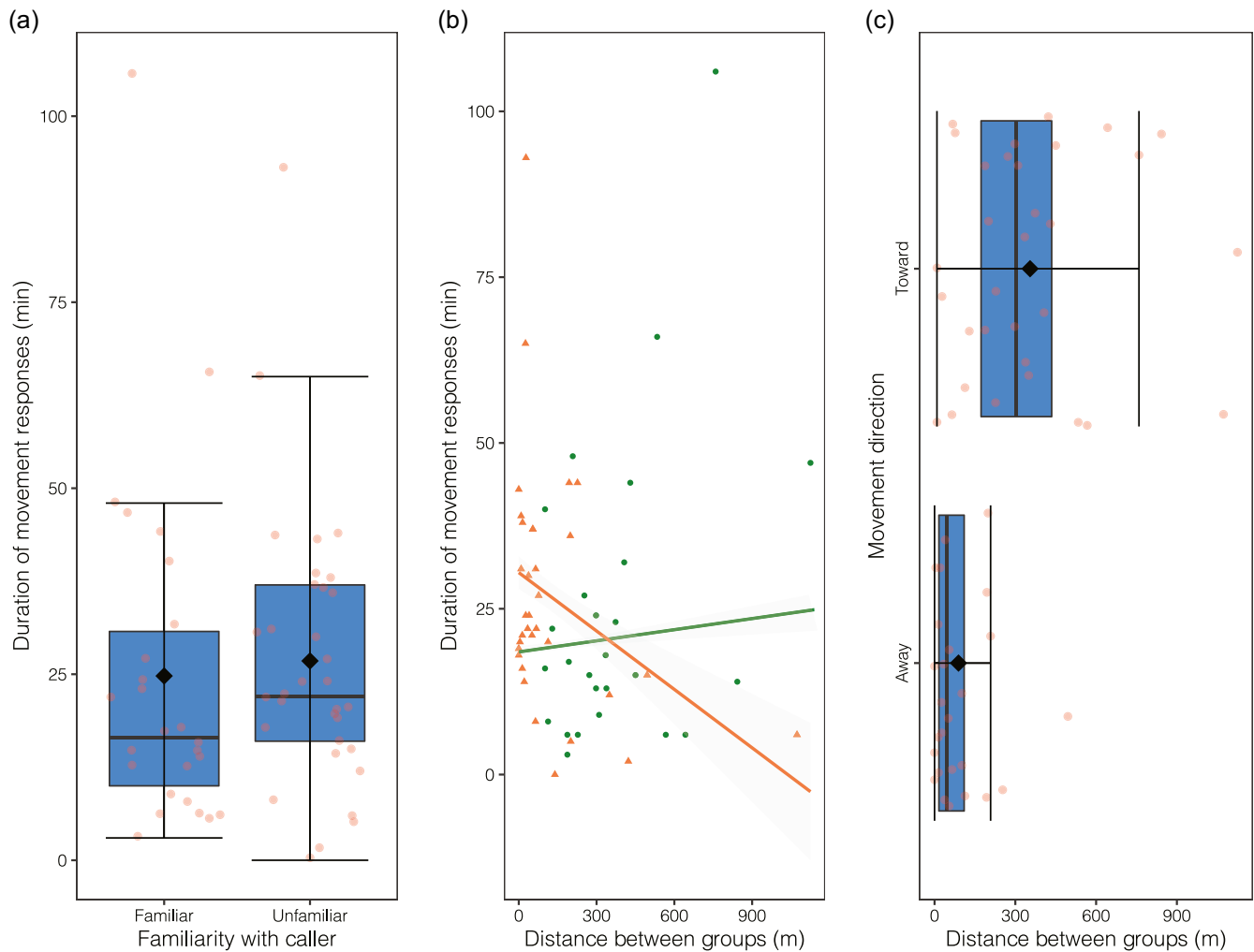
**FIGURE 2** Vocal responses of mantled howler monkeys to loud calls from neighbors in three groups studied at La Flor de Catemaco (Mexico) between January 2016 and March 2017: (a) latency to vocal responses in relation to familiarity with the caller; (b) duration of vocal responses in relation to familiarity with the caller; (c) distance between groups; (d) the interaction between familiarity with the caller and food availability; and (e) the interaction between familiarity and distance between groups. In (a) and (b), thick lines inside the boxes are the medians, black diamonds are the means, box limits are the 25th and 75th percentiles, whiskers indicate 1.5 × interquartile ranges, and data points are plotted as red circles. In (c) and (e), shaded areas in light gray are the 95% confidence intervals. In (d), unfamiliar group dyads are depicted with orange triangles and boxes whereas familiar group dyads are depicted with green circles and boxes. In (e), unfamiliar group dyads are depicted with orange triangles and lines whereas familiar group dyads are depicted with green circles and lines

recorded in the present study may function to defend valuable resources.

G3 arrived at La Flor de Catemaco from an adjacent area and established its home range within the home range of G1 and G2, which evidently resulted in a potential decrease in food availability for the resident groups. It is important to note that food biomass does not vary considerably at La Flor de Catemaco throughout the year and that food availability is high compared with other locations (Cano-Huertes et al., 2017). This could explain why behavioral responses to loud calls were not associated with food availability per se, as observed in previous studies (Hopkins, 2013; Van Belle & Estrada, 2019). Still, when food availability decreased, vocal responses to loud calls from unfamiliar residents were longer. It is,

therefore, possible that, even where food availability is relatively high and stable, groups defend food sources from unfamiliar neighbors. Alternatively, food defense through vocalizations could be a by-product of mating defense strategies, whereby males aim at retaining resident females and attract extra-group females by securing food resources (Fashing, 2001; Harris, 2006).

The behavioral responses of mantled howler monkeys to neighbor loud calls were also linked to the distance between groups. Long vocal responses and retreats from calling neighbors at short distances are consistent with contentions that by marking the occupation of an area and signaling group position to neighboring groups (da Cunha & Byrne, 2006; Van Belle et al., 2013) the loud calls of howler monkeys are a mechanism for the regulation of



**FIGURE 3** Movement responses to loud calls from neighbors in three groups studied at La Flor de Catemaco (Mexico) between January 2016 and March 2017: (a) duration of movement responses in relation to familiarity with the caller and (b) the interaction between familiarity with the caller and distance between groups; (c) direction of movement as a function of the distance between groups. In (a) and (c), thick lines inside the boxes are the medians, black diamonds are the means, box limits are the 25th and 75th percentiles, whiskers indicate  $1.5 \times$  interquartile ranges, and data points are plotted as red circles. In (b), unfamiliar group dyads are depicted with orange triangles and lines, familiar group dyads are depicted with green circles and lines, and shaded areas in light gray are the 95% confidence intervals

intergroup spatial organization (e.g., Chiarello, 1995; Chivers, 1969; da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Southwick, 1962). Furthermore, the long vocal and movement responses toward nearby unfamiliar neighbors suggest that the behavioral responses of groups receiving loud calls result from an integration of spatial and identity information (Kitchen, 2004; Kitchen, Horwich, et al., 2004; Sekulic, 1982; Sekulic & Chivers, 1986). Primate loud calls may have evolved under a variety of selective pressures (e.g., Burrows et al., 2016; Gustison et al., 2012; Mitani & Stuht, 1998). Thus, it is not surprising that loud calls are produced in several contexts and may have different functions (e.g., Cheney et al., 1996; Fashing, 2001; Pollock, 1986; Wich & Nunn, 2002).

Although we have framed this study around familiarity between neighboring groups, it is plausible that differences in response behavior are related to other factors. For example, our results are

consistent with variation in response being related to numerical odds in the number of adult males between groups. In our study, familiarity and male numeric odds covaried: even odds corresponded to the dyad composed of the two groups that have lived together at La Flor de Catemaco since 2005 (G1 and G2) and favorable and unfavorable odds were represented by interactions between those groups and G3. It remains for future research to evaluate the relative effects of familiarity and male numeric odds on the behavioral responses of mantled howler monkeys to neighbor loud calls.

In sum, the behavioral responses of mantled howler monkeys to loud calls from their neighbors were mainly influenced by familiarity between groups, such that stronger responses were recorded toward unfamiliar compared with familiar neighbors. Groups also vocalized for longer toward unfamiliar neighbors when food availability and distance between groups decreased. Response vocalizations were longer and receiving groups retreated when the calling group was



closer. Thus, the behavioral responses of mantled howler monkeys to neighbor loud calls result from the integration of information pertaining to caller identity as well as to their ecological and spatial context.

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## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

## DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author upon reasonable request.

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