Received: 25 February 2022 | Revised: 31 May 2023 | Accepted: 23 June 2023
DOI: 10.1002/ajpa.24810

RESEARCH ARTICLE

AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists
WILEY

Behavioral responses of mantled howler monkeys to neighbor long-distance vocalizations

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Funding information
Consejo Nacional de Ciencia y Tecnología; Universidad Veracruzana, Grant/Award Numbers: 610411, 254217

Abstract

Objectives: Long-distance vocalizations are used by primates in a variety of contexts and may have different functions. The long-distance vocalizations of howler monkeys (*Alouatta* spp.) underlie the spatial regulation of neighboring groups and could be associated with the defense of food resources. Here, we test the hypothesis that the behavioral responses of mantled howler monkeys (*A. palliata*) to neighbor long-distance vocalizations are influenced by the potential for range defensibility while accounting for location within the home range and food availability.

Methods: We studied two groups for 13 months and a total of 888 h at La Flor de Catemaco (Mexico). Group 1 had a 92-ha home range and Group 2 had a 24-ha home range. We recorded vocalizations ($N = 178$ calls) and movements ($N = 74$ movements) of focal groups following long-distance vocalizations produced by their neighbors.

Results: Movement responses, but not vocal responses, were predicted by range defensibility, location, and food availability. As predicted, the group living in the smaller and more defendable range showed stronger movement responses than the group in the larger home range. These movement responses had a shorter latency and longer duration in more valuable spatial and temporal contexts (i.e., the core area and during periods of low food availability).

Conclusions: These results suggest that the tradeoff between the costs and benefits of range defense varies according to the interactions between home range size and both the spatial (core areas) and temporal (food availability) abundance of resources. Thus, the responses of mantled howler monkeys to neighbor long-distance vocalizations could be related to home range defensibility.

KEYWORDS
Alouatta, fruits, home range, intergroup competition, vocalizations

1 | INTRODUCTION

Long-distance vocalizations are a common type of intergroup interaction in mammals (e.g., Proboscidea: Langbauer, 2000; Carnivora: Pfefferle et al., 2007; Ungulata: Feighny et al., 2006; Cetacea: Risch et al., 2007), including primates (Wich & Nunn, 2002). Proximately, long-distance vocalizations signal the presence of the caller and when produced as choruses provide indication of group size (e.g., lions, *Panthera leo*: McComb et al., 1994; Grinnell et al., 1995; gray wolves, *Canis lupus*: Harrington & Mech, 1983). Ultimately, they may function to defend valuable resources, such as food (e.g., black crested gibbons, *Nomascus concolor*: Peng-Fei et al., 2009) or mates (e.g., chacma baboons, *Papio ursinus*: Kitchen et al., 2004) by warning away possible competitors. Therefore, the study of long-distance vocalizations may offer insights into factors that influence intergroup competition.

Howler monkeys (*Alouatta* spp.) produce long-distance vocalizations (da Cunha et al., 2015) in a variety of contexts, including travel initiation, encounters with predators, and encounters with extragroup individuals (Kitchen et al., 2015). Several studies have found correlations between these calls and food availability: individuals are more likely to move toward calling neighbors when the availability of highly nutritious food items decreases (fruits: Hopkins, 2013; Van Belle & Estrada, 2020; flowers: Hopkins, 2013); and when located at feeding sites, individuals call at higher rates and for longer than elsewhere (Van Belle et al., 2013a). The long-calling patterns of howler monkeys may thus be ultimately related to the defense of food resources. This is further supported by evidence that the spatial location of groups also influences the long-distance vocalization patterns of howler monkeys, although such evidence is inconsistent (Altmann, 1959; Bernstein, 1964; Bolt et al., 2020; Chiarello, 1995; da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Whitehead, 1989). For instance, whereas in one study long-distance vocalizations were more frequent in border than in non-border areas (*A. guariba*: da Cunha & Jalles-Filho, 2007), in a different study they were more frequent in central areas of the home range than elsewhere (*A. caraya*: da Cunha & Byrne, 2006).

The causes for these inconsistencies have not been explored. One possible explanation is variation in range defensibility within and among populations. Range defensibility pertains to the ability of individuals to actively move through an area to monitor and defend it from intruders (Mitani & Rodman, 1979). It has been operationalized using the *D index*, which is the ratio of mean daily ranging distances to the diameter of the home range (Mitani & Rodman, 1979), and when D exceeds 1, individuals may economically patrol their territory (Lowen & Dunbar, 1994; Mitani & Rodman, 1979). Several mantled howler monkey (*A. palliata*) groups have $D \geq 1$, suggesting that they could defend their home ranges (Asensio et al., 2018). The extent of variation in range defensibility in this species is however notable. This is most likely linked to the fact that daily ranging distances are quite similar across populations whereas home range sizes vary as a function of habitat availability (e.g., Bicca-Marques, 2003; Crockett & Eisenberg, 1987; Fortes et al., 2015). Therefore, the influence of location within the home range on long-distance vocalization patterns is probably mediated by home range size, reflecting range defensibility.

In this study we focused on two mantled howler monkey groups and examined the hypothesis that their behavioral responses to neighbor long-distance vocalizations depended on the potential for range defensibility (proxied via home range size), while accounting for spatial location within the home range and food availability. We tested three predictions of this hypothesis. First, we predicted that the intensity of behavioral responses to neighbor long-distance vocalizations should increase with decreasing home range size. Specifically, the group in the smaller, more defendable home range should be more likely to display vocal and movement responses to neighbor long-distance vocalizations, which should additionally be more immediate and lengthier. During movement responses the group should move farther and be more likely to approach the neighboring caller. Second, given the higher potential for range defensibility in small home ranges and that food sources located in overlapping areas of the home range are more likely to be contested by neighbors than those in core areas, we also expected stronger responses (as described for the first prediction) to neighbor calls in overlapping and non-core areas than in the core areas by the group living in a small home range. Third, as food abundance is expected to be positively related to home range size, we predicted stronger behavioral responses by the group living in a small home range when food availability is low.

2 | METHODS

2.1 | Ethics statement

Our study complied with the American Society of Primatologists Code of Best Practices in Field Primatology (ASP, 2014) and Principles for Ethical Treatment of Non-Human Primates (ASP, 2021). 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

From January 2017 to January 2018, we conducted the study at La Flor de Catemaco (18°26′43″N, 95°02′49″W), located in Veracruz, Mexico. La Flor de Catemaco is a private property that includes ca. 100 ha of tall evergreen forest. We studied two of the three groups that lived at the site (Figure 1). Group 1 comprised three adult males, three adult females, and one infant (4 months old by the end of the study) whereas Group 2 included three adult males, four adult females, and two infants (6 and 5 months old by the end of the study). Two more infants were born in Group 2 during the study (April and August) but were inferred to have died as they disappeared before 1 month of age. By focusing on these two groups, we could test our predictions while accounting for several factors that influence long-distance vocalization patterns in howler monkeys: familiarity (Briseño-Jaramillo et al., 2015; Ceccarelli et al., 2021; Hopkins, 2013), as these groups had been residents for 13 years, whereas the third group arrived at the site 2 years before the beginning of the study; home range stability (Kitchen, 2004), given that the two groups had occupied approximately the same home ranges since 2005 and had adjacent home ranges; and male numerical odds (Kitchen, 2004), as both groups had the same number of males. Both groups also had the same number of neighboring groups (i.e., two) and the same likelihood of receiving long-distance vocalizations from other groups, both from within and outside La Flor de Catemaco. At La Flor de Catemaco only males routinely participate in long-distance vocalization bouts, whereas females occasionally join males in choruses associated with alarm contexts (e.g., in response to anthropogenic noise).

2.3 | Behavioral data collection

All subjects were fully habituated to the presence of researchers and were easily recognized through physical characteristics. From January 2017 to January 2018, we observed each group once per month for 4 days during a one-week period, usually during complete day follows (06:00–07:00 to 17:00–18:00 h, depending on the time of the year). During each observation day, we recorded all occurrences (Altmann, 1974) of long-distance vocalizations (i.e., roars, barks, and "oodles": da Cunha et al., 2015), produced by neighbors or by the focal group, either by one or several (i.e., chorus) individuals. We recorded with a Global Positioning System receiver (GPS) the geographic location of the focal group when producing or receiving a long-distance vocalization. We also recorded all occurrences of movement by any adult group member beyond 5 m of its original position following a long-distance vocalization by another group. We recorded the location of the first individual that moved (i.e., geolocated it each time it moved to a different tree) using a GPS unit, until it did not move for 10 min. We collected a total of 888 h of observations (group 1: 432, group 2: 456).

2.4 | Home range estimation

We used historical data to describe the areas of the groups' home ranges (i.e., core, non-core, and overlap) before the beginning of behavioral data collection. Specifically, we used location data collected continuously (i.e., each time individuals moved to a different tree) with a GPS during the two rainy and the two dry seasons preceding behavioral observations (i.e., from December 2014 to December 2016). For Group 1 we obtained 5830 geographic location points recorded during 678.8 h of observations, and for Group 2 we obtained 5806 geographic location points recorded during 703.8 h of observations. Based on these data we estimated the home range of each group in R 4.2.0 (R Core Team, 2022) as the fixed Kernel densities at 95% probability of use and the core areas as fixed Kernel densities at 50% probability of use (Samuel & Green, 1988; Seaman & Powell, 1996). In these calculations we used the base settings of the R package 'adehabitatHR' (Calenge, 2021), including the mean squares function. From December 2014 to November 2016, Group 1 had a 92-ha home range with a 24-ha core area and Group 2 had a 19-ha home range with a 4-ha core area (Figure 1). We defined overlap areas as those that were part of the home ranges of both groups,

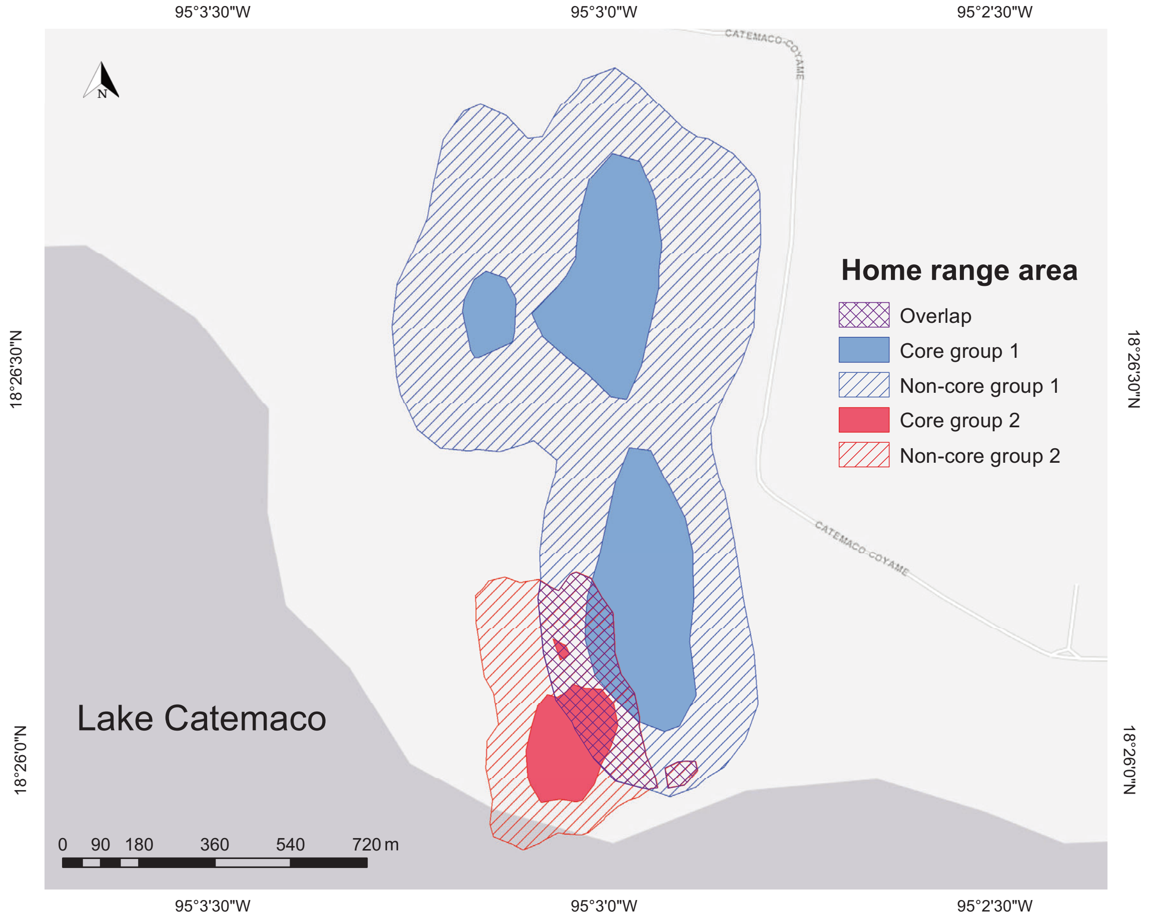

FIGURE 1 Home ranges of the two mantled howler monkey groups studied at La Flor de Catemaco (Los Tuxtlas, Veracruz, Mexico) from December 2014 to December 2016. A third group lived in the site to the west of the study groups' home ranges. Home ranges correspond to 95% Kernel density contours and core areas to 50% contours.

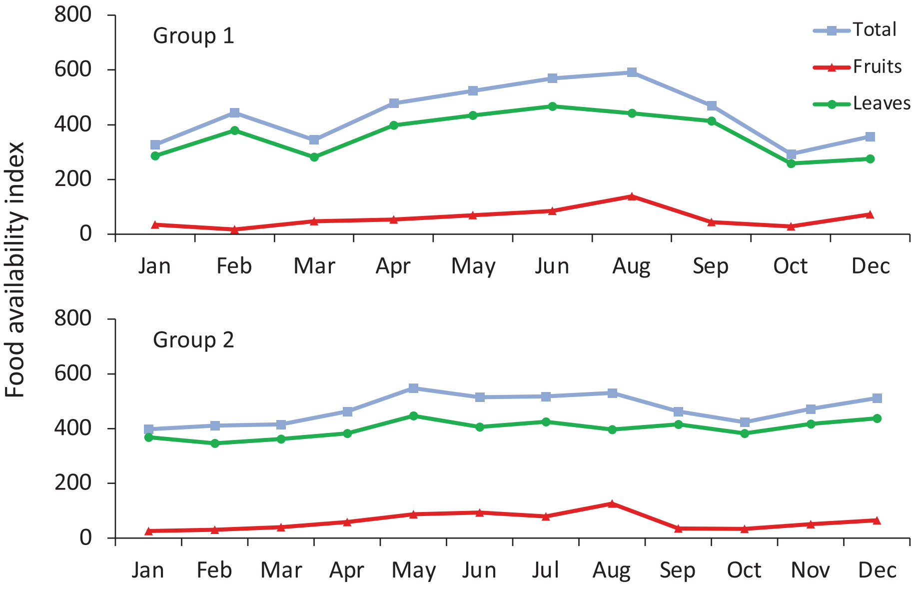

FIGURE 2 Variation in leaf (green), fruit (red), and total food abundance (blue) for two groups of mantled howler monkeys at La Flor de Catemaco (Los Tuxtlas, Veracruz, Mexico) from January 2017 to January 2018 as assessed with a food availability index (see text). Total food abundance is the sum of fruit, leaf, and flower abundance.

and non-core areas as those that were neither core nor overlap areas. The home ranges of the two groups overlapped in two areas (8 ha) which we classified as overlap core and overlap non-core. As the mean ± SD home range size of mantled howler monkeys is 33.5 ± 23.7 ha (Fortes et al., 2015), the home range of Group 1 may be considered relatively large (i.e., lower defensibility) whereas that of Group 2 is relatively small (i.e., higher defensibility).

2.5 | Food availability estimation

To estimate food availability, we used a food availability index (Chaves & Bicca-Marques, 2016), which integrates both spatial and temporal variation in potential food resources. To determine spatial variation in food availability, following the zoning of the home ranges of the two groups, we identified feeding trees in core, non-core, and overlap areas using the Gentry method (Gentry, 1982). Accordingly, in each area of the home range we plotted 10 randomly distributed transects of 2 × 50 m (Gentry, 1982). In each transect we identified all trees reported as food sources for howler monkeys to species level (Dias & Rangel-Negrín, 2015). We measured the diameter at breast height of each tree to calculate its basal area. We then calculated importance value indices (IVI) per home range area per plant species by adding plant density (number of trees/1000 m^2), frequency (number of transects with the species/1000 m^2), and dominance (sum of basal areas in the 1000 m^2).

To determine temporal variation in food availability, during the behavioral sampling period (January 2017 to January 2018) we assessed the abundance of plant items each week in 397 feeding trees (determined via long-term observations of the population) randomly distributed within the home ranges of both groups. Specifically, we estimated the abundance of fruits (ripe and unripe), leaves (mature and young), and flowers on a categorical scale: 0 = absence of the item; 1 = presence of the item between 1% and 25% of the total potential canopy coverage; 2 = 26%–50%; 3 = 51%–75%; 4 = 76%–100% (Fournier, 1974). With these data, we calculated mean monthly abundance scores per plant item (Figure 2). We multiplied IVI by monthly abundance scores per plant species and summed all species values per home range area to obtain an estimation of food abundance per month per home range area. In data analysis, we focused on total food availability calculated as the sum of monthly abundance scores of all plant items.

2.6 | Data organization and analysis

To determine which vocalizations and movements by focal groups would be classified as responses to neighbor long-distance vocalizations, we first identified in our dataset all long-distance vocalizations that were heard by human observers following the focal groups ($n = 448$). We identified and excluded all cases in which a neighbor loud call was followed by other stimuli before focal groups produced long-distance vocalizations ($n = 270$) or movements ($n = 374$). These stimuli included the presence or vocalizations of other species (e.g., coatis, *Nasua narica*; plain chachalacas, *Ortalis vetula*), anthropogenic noise (e.g., traffic, tools), and geophony (e.g., rain, thunder). We then calculated the latency between each received long-distance vocalization and the first vocalization and the first movement by the focal group, resulting in 178 vocalizations, (latency of 0–286 min) and 74 movements (latency of 0–303 min). We compared these latencies with the latency between a control point and the occurrence of a vocalization or movement by the focal group (matched control samples, MC hereafter) with survival analysis using the Kaplan–Meier estimate. Control points were the starting times of sampling sessions, and we selected 64 MC for vocalizations and 33 MC for movements, which were the total number of sessions in which no stimuli (as described above) were recorded before a vocalization and movement by the focal group following the onset of the sampling session.

We inspected the resulting life tables and identified the first overlap of the 95% confidence intervals (CI) of the hazard rates of latencies to behaviors following MC and following neighbor long-distance vocalizations. We considered such overlap as the timeframes in which the likelihood that mantled howler monkeys responded to a neighbor long-distance vocalization was not different from the likelihood that they displayed vocalizations or movements in response to other stimuli. The 95% CI of latencies to vocalizations overlapped after 14 min (Kaplan–Meier survival estimate MC = 0.67 ± 0.06, 95% = 0.55–0.78; Kaplan–Meier survival estimate post-neighbor long-distance vocalizations = 0.77 ± 0.03, 95% CI = 0.71–0.83) and that of latencies to movements overlapped after 35 min (Kaplan–Meier survival estimate MC = 0.71 ± 0.08, 95% = 0.63–0.84; Kaplan–Meier survival estimate post-neighbor long-distance vocalizations = 0.85 ± 0.04, 95% CI = 0.79–0.92). Based on these timeframes, we classified 88 vocalizations and 41 movements as responses to neighbor long-distance vocalizations and 90 vocalizations and 33 movements as non-responses.

We used the initial and final geographic location of movement responses to neighbor long-distance vocalizations to determine the movement distance and to draw an imaginary line that defined the direction of the movement. Given that we did not know the exact location of the calling group and that due to the spatial configuration of the forest the two groups could only come into contact through a strip of vegetation in the overlapping area, we classified each movement response according to its position with respect to that passage. Thus, we classified movements ≤45° in the direction of the passage as toward the potential conflict zone, movements ≥135° as away, and movements in other directions as neutral (Van Belle & Estrada, 2020).

We conducted all statistical analyses with R 4.2.0 (R Core Team, 2022). We built 10 generalized linear models to test our predictions with the following predictors: group identity (a proxy for home range size; categorical variable with two levels, Group 1 and Group 2; first prediction); the interaction between group identity and the location of groups in their home ranges when receiving long-distance calls (categorical variable with three levels, that is, core, noncore, and overlap, with core and noncore overlaps combined due to <5 observations for Group 2; second prediction); and the interaction between group identity and food availability (third prediction).

In the first two models we analyzed the occurrence of behavioral responses with binomial generalized linear models (GLM) in which vocal and movement responses were coded as binary variables (yes/no). In these models, vocal and movement responses that occurred outside the timeframes defined by the survival analysis were coded as non-responses. To analyze variation in the latency and duration (in minutes) of both vocal and movement responses to neighbor long-distance vocalizations (models three to six) we ran GLMs with either Poisson (latency to movement responses) or negative binomial (all other latency and duration variables) error distributions (function 'glm.nb' in R package 'MASS': Ripley, 2022a). To analyze the distance of movement responses (in m; seventh model) we used a GLM with a Gaussian error distribution. Regarding the direction of movement responses (i.e., toward, away, or neutral), the small sample of movement responses that we collected resulted in insufficient degrees of freedom to include all predictors in a single model. Thus, we ran three different multinomial GLMs (models 8–10), one for each predictor ('multinom' function in R package 'nnet': Ripley, 2022b).

We standardized food availability variables to a mean of 0 and a standard deviation of 1. We verified the underlying assumptions of models visually with *Q*–*Q* plots of residuals fitted against predicted values. Given the small sample size ($N < 200$ in all models) with respect to the number of predictors, we diagnosed model stability via the inspection of DFBETAS which indicated that model results were not affected by influential cases. We calculated pseudo coefficients of determination of models as effect size measures ('r2' function in R package 'performance': Lüdecke, 2022) and for significant predictors we ran pairwise comparisons with contrast analysis (with Tukey adjustment). No collinearity was detected between group identity and other predictors in all models (i.e., generalized variance inflation factors <2).

3 | RESULTS

We recorded 178 long-distance vocalizations from neighbors, of which 49% elicited vocal responses from focal groups within the first 14 min with a mean ± SD latency of 4.9 ± 5.1 min, and these responses lasted 2.1 ± 1.9 min. Of the 74 neighbor long-distance vocalizations that were associated with a movement response, 55% occurred during the first 35 min after a call, with a mean latency of 13.2 ± 11.2 min, and lasted 22.1 ± 25.5 min. When focal groups moved following a neighbor's long-distance vocalization, they moved 221.1 ± 271.72 m. When hearing a neighbor's long-distance vocalization, focal groups were usually in core ($n = 15$) and non-core areas ($n = 15$), followed by overlap areas ($n = 11$; Figure 4). The most frequent direction of movement by focal groups was toward calling groups, followed by movements away, and neutral (Figure 4). When approaching a calling neighbor, focal groups moved 235.1 ± 243.1 m whereas when retreating or moving in neutral direction they moved 283.3 ± 341.0 m and 141.3 ± 95.9 m, respectively.

The vocal responses of mantled howler monkeys to neighbor long-distance calls were not influenced by group identity (contradicting the first prediction) nor by its interaction with either area of the home range when receiving calls (contradicting the second prediction) or food availability (contradicting the third prediction; Table 1). Similarly, neither the occurrence nor the distance of movement responses to neighbor calls were influenced by the predictors (Table 2).

However, Group 2, the group living in a smaller, more defendable home range, displayed more immediate and longer movement responses to neighbor's long-distance vocalizations when it was in the core are of its home range than all other group/area combinations, supporting the second prediction (estimates ± SE of Tukey contrasts for latency: Group 1 core vs. Group 2 core = 2.07 ± 0.5, Group 1 non-core vs. Group 2 core = −1.83 ± 0.5, Group 1 overlap vs. Group 2 core = 2.03 ± 0.6, Group 2 core, vs. non-core = −2.14 ± 0.6, Group 2 core vs.

TABLE 1 Results of generalized linear models (ANODE) of the factors influencing the vocal responses of mantled howler monkeys (*Alouatta palliata*) to neighbor long-distance vocalizations ($n = 178$ vocalizations).

Variable/term	R^2	χ^2	p
Occurrence (binomial)[a]	0.04		
Group identity		0.47	0.489
Group identity × location within home range		2.33	0.674
Group identity × food availability		3.15	0.207
Latency (negative binomial)	0.03		
Group identity		0.01	0.903
Group identity × location within home range		1.69	0.792
Group identity × food availability		0.26	0.879
Duration (negative binomial)	0.03		
Group identity		2.11	0.146
Group identity × location within home range		1.51	0.468
Group identity × food availability		1.41	0.234

[a] Family distribution used in each model indicated in parenthesis.

TABLE 2 Results of generalized linear models (ANODE) of the factors influencing the movement responses of mantled howler monkeys (*Alouatta palliata*) to neighbor long-distance vocalizations ($n = 74$ vocalizations).

Variable	R^2	χ^2	p
Occurrence (binomial)[a]	0.11		
Group identity		0.55	0.456
Group identity × location within home range		6.72	0.151
Group identity × food availability		0.18	0.910
Latency (Poisson)	0.18		
Group identity		5.88	0.052
Group identity × location within home range		10.45	0.034
Group identity × food availability		21.5	<0.001
Duration (negative binomial)	0.20		
Group identity		1.35	0.244
Group identity × location within home range		11.76	0.020
Group identity × food availability		6.78	0.034
Distance (Gaussian)	0.17		
Group identity		2.23	0.135
Group identity × location within home range		3.21	0.522
Group identity × food availability		0.93	0.629
Direction (multinomial)[b]			
Group identity	0.02	0.68	0.710
Group identity × location within home range	0.28	11.22	0.041
Group identity × food availability	0.16	6.03	0.197

[a] Family distribution used in each model indicated in parenthesis.
[b] The influence of each predictor on this behavioral response had to be examined in independent models due to small degrees of freedom.

overlap $= -1.50 \pm 0.2$; duration: Group 1 core vs. Group 2 core $= -2.87 \pm 0.7$, Group 1 non-core vs. Group 2 core $= -2.13 \pm 0.7$, Group 1 overlap vs. Group 2 core $= -2.08 \pm 0.5$, Group 2 core, vs. non-core $= -1.98 \pm 0.5$, Group 2 core vs. overlap $= -1.60 \pm 0.5$; $p < 0.05$ for all pairwise comparisons; Figure 3a,c). In both groups, latencies to movement responses decreased with increasing food abundance, but this relationship was stronger for Group 2 (supporting the third prediction; Figure 3b). Whereas the time Group 1 spent moving in response to neighbor long-distance call was not influenced by food availability, Group 2 spent more time moving when food availability was lower (third prediction; Figure 3d). Regarding the direction of movement, Group 2 was more likely to move toward than away or neutrally from calling neighbors when it was in the core area of its home, contradicting the second prediction (estimates ± SE of Tukey contrasts: Group 2-core-toward vs. Group 2-core-away $= 5.13 \pm 0.9$, Group 2-core-toward vs. Group 2-core-neutral $= 4.83 \pm 0.8$; $p < 0.05$ for both pairwise comparisons; Figure 4).

4 | DISCUSSION

We investigated if the behavioral responses of mantled howler monkeys to long-distance vocalizations produced by neighboring groups were related to the potential for home range defensibility (proxied via home range size) while accounting for the location of groups within their home ranges and for food availability. Contrary to our first prediction, home range size per se (proxied via group identity) did not influence behavioral responses. Regarding the second (interaction between home range size and location) and third (interaction between home range size and food availability) predictions, we did not find any consistent pattern of vocal responses to neighbor long-distance vocalizations, but several measures of group movement were affected by the examined predictors. Specifically, compared with Group 1, Group 2 (smaller home range) displayed more immediate and longer movement responses to neighbor calls when it was in the core area of its home range and when food availability decreased. Additionally, when in the core area of its home range, Group 2 tended to approach a calling neighbor. Given that only two groups were studied and the small number of vocal and movement responses that were analyzed, caution should apply in interpreting these results, which could be considered preliminary. Yet this evidence suggests that the behavioral responses of mantled howler monkeys to neighbor long-distance vocalizations could be related to range defensibility.

Several howler monkey species could be territorial based on range defensibility (Asensio et al., 2018), but there is little direct evidence of resource defense or home range patrolling. Here, we demonstrate that the group with smaller home range displayed movement responses that are consistent with range defense, suggesting that previous inconsistencies in the analysis of range defensibility (Asensio

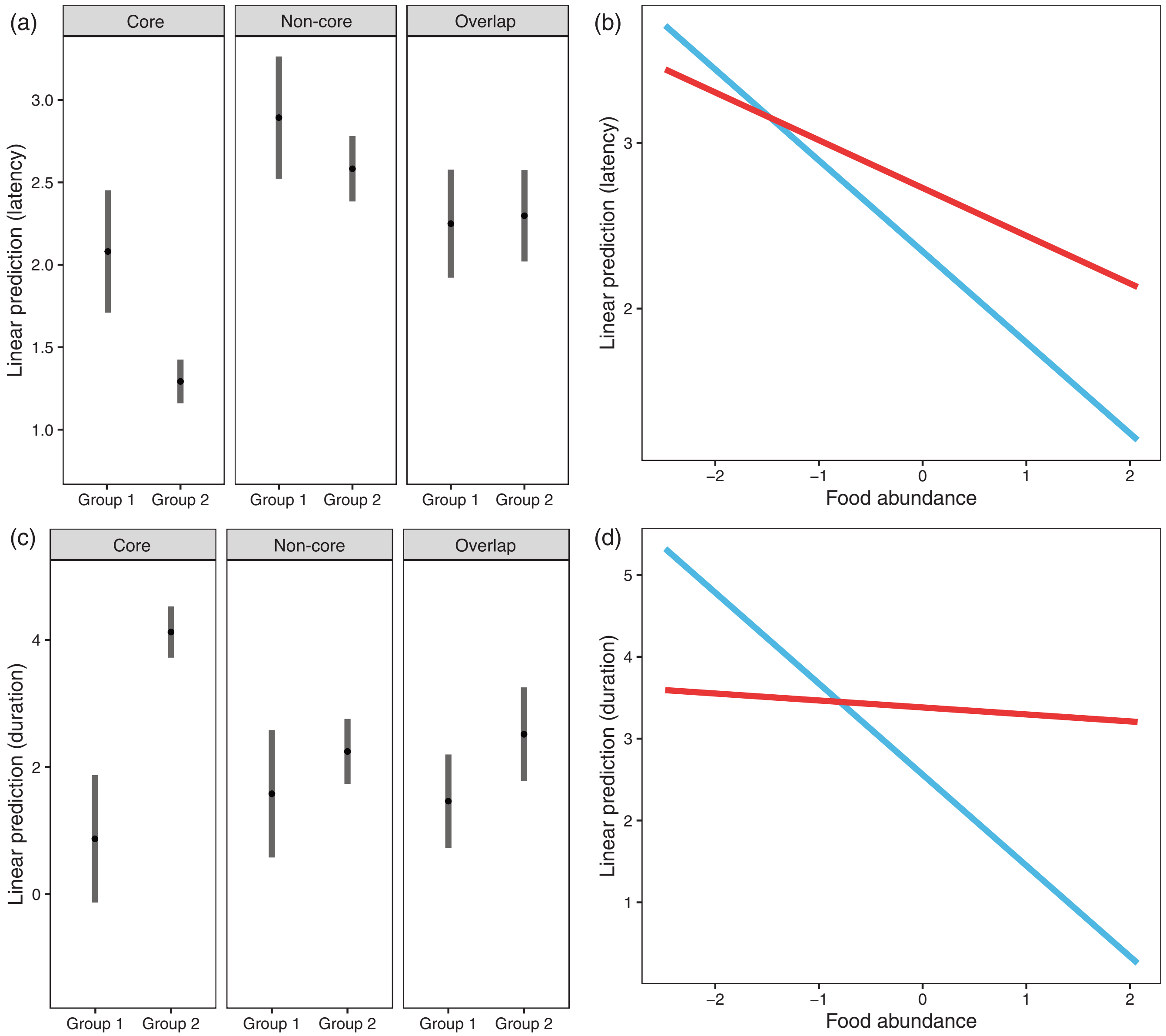

FIGURE 3 GLM results of the influence of the interaction between group identity and area of the home range where groups were located when receiving long-distance vocalizations from neighbors (a,c) and of the interaction between group identity and food availability (b,d) on the latency and duration of movement responses. In (a) and (c) black dots and gray rectangles are model estimates and their 95% confidence intervals, respectively. In b and c, the red lines correspond to Group 1 (larger, less defensible home range) and the blue lines to Group 2 (smaller, more defensible home range).

et al., 2018) could result from intraspecific variation in home range size. The movement responses of the group with the smaller, more defensible home range after neighbor long-distance calls are consistent with a pattern of core defense, which has been reported in several primates and results from a higher abundance of resources in these areas than elsewhere in the home range (e.g., Crofoot et al., 2008; Harris, 2006; Waser & Wiley, 1979). Additionally, the group with the smaller home range comprised more individuals (i.e., lower per capita food availability), which could further the importance of defending their home range (Pearce et al., 2012). The displaying of movement rather than of vocal responses to neighbor long-distance calls is unexpected given the characteristic energy-saving ecological strategy of the genus (e.g., goal-directed travel, long resting periods, behavioral thermoregulation: Milton, 1998) and contentions that long-distance vocalizations should be less energetically expensive than patrolling (e.g., Amsler, 2009; Mitani, 1987; Pourier, 1968). Nevertheless, listeners move toward callers in both howler monkeys (Chiarello, 1995; da Cunha & Jalles-Filho, 2007; Hopkins, 2013; Van Belle & Estrada, 2020) and other primates (Robinson, 1979). In this context, our results suggest that the tradeoff between the costs and benefits of range defense varies as a function of the interactions between home range size and both the spatial (core areas) and temporal (food availability) abundance of resources, as observed in other primate species (Brown, 2013).

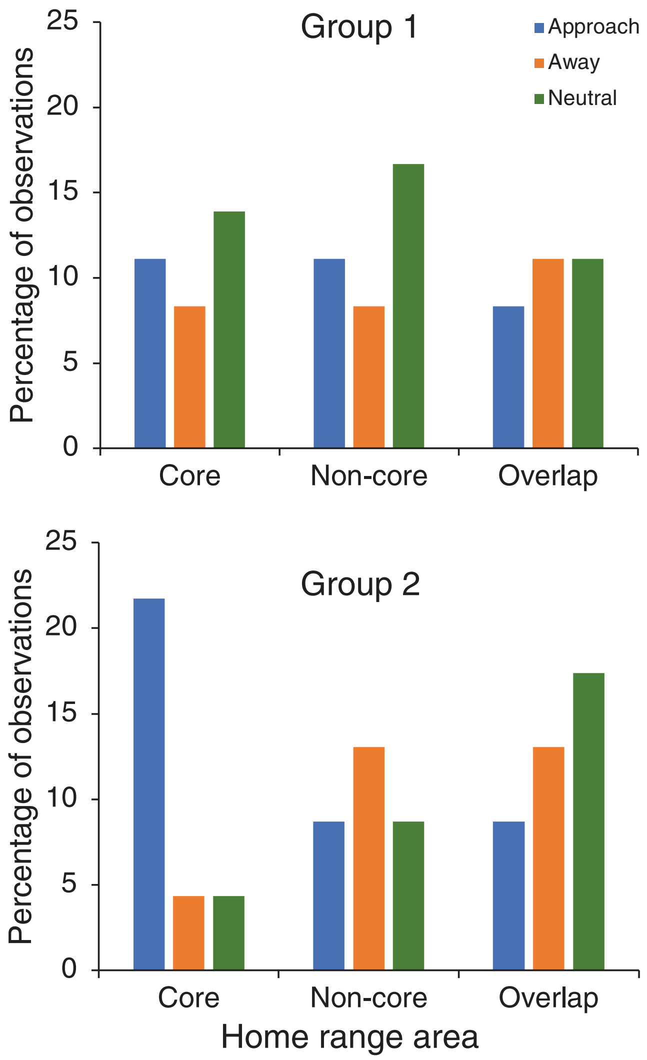

FIGURE 4 Variation in the direction of movement responses by mantled howler monkeys to neighbor long-distance vocalizations according to group identity and area of the home range where groups were located when receiving calls.

Although mantled howler monkeys did respond often to long-distance vocalizations from their neighbors, the absence of consistent vocal responses depending on home range size, location, and food availability suggests that at La Flor de Catemaco mantled howler monkeys do not vocally reciprocate as a function of the risk of encounters or resource value. One possible explanation for this absence is a "dear enemy" effect, whereby groups reduce behavioral responses toward known rivals (Ydenberg et al., 1988). Additionally, it has been suggested that the long-distance vocalizations of howler monkeys may be proximately linked to intergroup spatial regulation (e.g., Ceccarelli et al., 2019; da Cunha & Byrne, 2006; Whitehead, 1987). Through the advertisement of occupancy (Waser & Wiley, 1979), long-distance vocalizations allow for mutual avoidance among neighbors (Baldwin & Baldwin, 1976; da Cunha & Byrne, 2006; Van Belle et al., 2013b; Whitehead, 1987) thus preventing potentially risky intergroup encounters, which in this species may result in injury or death (Cristóbal-Azkarate et al., 2004). Accordingly, during the study period the two groups never interacted with physical contact and were within sight of each other (<50 m) on only five occasions. In this context, the absence of vocal responses to neighbors in our study may be related to the low population density at Flor de Catemaco compared to other sites (Cano-Huertes et al., 2017): population density at La Flor de Catemaco (35 individuals/km^2) is less than half of that reported for Barro Colorado Island, Panama (80 individuals/km^2: Milton, 1996) or La Suerte, Costa Rica (109 individuals/km^2: Bolt et al., 2022). Future research based on a larger sample of groups and populations should aim at parsing the relative effects of home range size, food abundance, and population density on the vocal responses of mantled howler monkeys to neighbor long-distance vocalizations. This will allow a better understanding of the functions of long-distance calls in this species.

Long-distance vocalization patterns in howler monkeys are highly variable (i.e., when, where, and who calls: Kitchen et al., 2015), probably due to past (e.g., familiarity: Ceccarelli et al., 2021), present (e.g., food availability, male numeric odds, presence of vulnerable offspring: Hopkins, 2013; Kitchen, 2004), and future (e.g., group transfer prospects: Clarke & Glander, 2010) constraints on individual behavior. The current study accounted for the first two, whereas the putative effect of the latter remains to be assessed. In this study system, movement responses of mantled howler monkeys to neighbor long-distance vocalizations vary between groups as a function of location within the home range and food availability and could be linked to resource defense.

AUTHOR CONTRIBUTIONS

Natalia Maya Lastra: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Ariadna Rangel Negrín:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); project administration (equal); resources (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal). **Pedro A. D. Dias:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

ACKNOWLEDGMENTS

We thank P. Cruz Miros and several volunteers and students for their invaluable help during fieldwork. La Flor de Catemaco granted permission to work at this site, and we thank Ing. J. L. Ponce Puente for facilitating our work in a variety of ways. We thank F. Aureli, an Editorial Board member of AJBA, and two anonymous reviewers for valuable input on previous versions of the manuscript. A. Rangel-Negrín and P. A. D. Dias thank Mariana and Fernando for constant support and inspiration to study primate behavior. This study was supported by Universidad Veracruzana and Conacyt (beca de maestría 610411; proyecto ciencia básica 254217). A. Rangel-Negrín and P. A. D. Dias were supported by a grant to CA-UV-25 from the Dirección General de Desarrollo Académico e Innovación Educativa, Universidad Veracruzana (México) while preparing this manuscript.

DATA AVAILABILITY STATEMENT

The study data are available from the corresponding author upon reasonable request.

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How to cite this article: Maya Lastra, N., Rangel Negrín, A., & Dias, P. A. D. (2023). Behavioral responses of mantled howler monkeys to neighbor long-distance vocalizations. *American Journal of Biological Anthropology*, 1–10. https://doi.org/10.1002/ajpa.24810