International Journal of Primatology (2019) 40:197–213
https://doi.org/10.1007/s10764-018-0075-1

An Exploration of the Factors Influencing the Spatial Behavior of Mantled Howler Monkeys (*Alouatta palliata*)

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Received: 11 August 2018 / Accepted: 15 November 2018 / Published online: 10 December 2018

Abstract

Space use patterns are the result of complex interactions between individuals and their environment. Although competition with conspecifics, the distribution and availability of food resources and climatic conditions may all influence space use by primates, these factors are usually addressed separately. Studies that integrate social, ecological, and physical factors have the potential to improve our understanding of variation in the spatial behavior of primates. We studied two groups of mantled howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico, to explore how intergroup competition, food availability, and ambient temperature influenced their use of space over 15 months. Loud calls produced by neighboring groups were a determining factor in the variation in the area used per month, daily ranging distance, and travel rate. Food availability did not influence any aspect of spatial behavior, but the distribution of feeding trees affected travel rate. Ambient temperature influenced the frequency and speed of travel. These results suggest that the spatial behavior of howler monkeys is influenced by social (intergroup competition), ecological (food distribution), and physical (ambient temperature) factors, and that the specific effects of these factors vary among measures of space use.

Keywords Competition · Loud calls · Platyrrhini · Ranging · Spatial behavior · Temperature · Travel

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Handling Editor: Joanna M. Setchell

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Introduction

The use of space is the result of complex interactions between an individual and the spatial and temporal characteristics of the environment (Nathan *et al.* 2008). Although variation in the use of space by primates has been usually linked to the distribution and availability of food resources (Chapman *et al.* 2012), there is evidence that competition with conspecifics (e.g., Crofoot *et al.* 2008; Noser and Byrne 2007), other ecological characteristics of the habitat (e.g., predation: Matsuda *et al.* 2009), and climatic conditions (e.g., Watanuki and Nakayama 1993) are also influential in spatial behavior.

Competition, within and between species, is an ecological interaction between two or more individuals in which fitness may be reduced as a result of the presence of others (Darwin 1859; Krebs and Davies 1993). The ability of a group to acquire and defend resources has been proposed as a selective force for the evolution of group life (Krebs and Davies 1993; Packer *et al.* 1990) and the presence of neighboring groups of conspecifics influences the spatial behavior of gregarious species (Bolyard and Rowland 2000; Gese 2001; Kitchen 2000; Kitchen *et al.* 2004; Lazaro-Perea 2001). In many mammalian species, competitive interactions between individuals or groups are mediated by the production of long-distance calls (hereafter, loud calls; Proboscidea: Langbauer 2000; Carnivora: Mitchell *et al.* 2006; Pfefferle *et al.* 2007; Ungulata: Feighny *et al.* 2006; Cetacea: Risch *et al.* 2007; Saulitis *et al.* 2005; Primata: Oliveira and Ades 2004; Wich and Nunn 2002). Loud calls may be used for signaling the occupation of a territory, (e.g., lions [*Panthera leo*]: Grinnell *et al.* 1995; McComb *et al.* 1994; gray wolfs [*Canis lupus*]: Harrington and Mech 1983), defending a food source (e.g., black crested gibbons [*Nomascus concolor*]: Peng-Fei *et al.* 2009), or defending potential mating partners (e.g., yellow baboons [*Papio hamadryas*]: Kitchen *et al.* 2004). The strong selective pressure on vocal communication determines a great variety of vocalizations depending on their context of occurrence (Alcock 1997; Cheney and Seyfarth 2003). Nevertheless, very few studies have linked loud calls among groups with their spatial behavior.

There is also evidence of covariation between diet and space use patterns, which is linked to ecological parameters, such as the abundance, distribution, and quality of food resources (e.g., Hurtado *et al.* 2017; Saj and Sicotte 2007), or the presence of competitors and/or predators (e.g., Asensio *et al.* 2018; Dussault *et al.* 2005; Gorini *et al.* 2012; Laundré *et al.* 2001). Individuals may respond to the reduction of the availability of preferred foods by decreasing locomotion time and distance traveled; feeding on elements of lower nutritional value and energy (i.e., low cost/low reward strategy); or increasing the traveled distance in search of high-quality food (high cost/high reward strategy) (Buzzard 2006; Doran 1997; Gurski 2000).

Behavioral energy conservation strategies in wild animals are also determined by climatic conditions (Bicca-Marques y Azevedo 2004; Prates y Bicca-Marques 2008). Animals have a thermoneutral range of ambient temperature, which coincides with the optimal temperature for organism function (Cabanac 2006), and allows molecular, physiological, and behavioral processes (Pörtner *et al.* 2006). An evolutionary response to temperature variation is thermoregulation, which in endotherms aims to maintain optimal and nearly constant body temperatures regardless of fluctuations in ambient temperature through the production of internal metabolic heat (Terrien *et al.* 2011). At lower ambient temperature, individuals use more energy to maintain body temperature

(Szekely *et al.* 2004; Westerterp 2004), and the high needs for increased thermogenesis during cold exposure can be behaviorally supported by an increase in motor activities (Aujard and Vasseur 2001) and in energy intake (Agetsuma 1995a, b; Westerterp-Platenga 1999). Conversely, when ambient temperature is higher than the thermoneutral range, individuals must operate against the heat gradient by avoiding exposure to high temperatures, decreasing activity and energy intake (Fan *et al.* 2008; Hanya 2004). Phenotypic flexibility in response to environmental seasonality is ubiquitous among animals (Mollusca: Bailey and Johnston 2005; Insecta: Bale 2002; Cricetidae: Rezende *et al.* 2004; Columbidae: McKechnie and Wolf 2004; Crocodylia: Seebacher *et al.* 2003; Bovinea: Owen-Smith 1994; Cheirogaleidae: Perret and Aujard 2001; Lemuroidea: Ganzhorn 2002), and there is ample evidence that thermal environment and the ability to cope with temperature fluctuations affect behavior, such as activity budgets, feeding, and movement (Baoping *et al.* 2009; Chiarello 1995a; Fernández-Duque 2003; Hanya 2004; Harrison 1985; Hill 2006; Nowack *et al.* 2013).

Howler monkeys (*Alouatta* spp.) are frugivore–folivore, arboreal, Neotropical primates that live in cohesive groups, usually containing several adult males and females, and immatures (Di Fiore and Campbell 2007). Adult individuals (mainly males) produce long, low-frequency calls that can be heard for over a kilometer (Horwich and Lyon 1990; Whitehead 1995). Most evidence suggests that loud calls are involved in the regulation of the use of space between neighboring groups (Chiarello 1995b; da Cunha and Byrne 2006; da Cunha and Jalles-Filho 2007; Kitchen 2000; Sekulic 1982; Whitehead 1987, 1989), as vocalizing individuals disclose their location to neighboring groups, enabling contact avoidance (Baldwin and Baldwin 1976; Whitehead 1987, 1989). Although energetically expensive, loud calls are less expensive than physical fights, which entail the risk of injury and even death (Cristóbal-Azkarate *et al.* 2004; Crockett and Pope 1988). Howler monkeys spend most of their daytime resting (Bicca-Marques and Calegaro-Marques 1994; Di Fiore and Campbell 2007; Estrada *et al.* 1999; Pinto *et al.* 2003). There is some evidence that howler monkeys use their space in relation to food availability, and several studies have shown that when the sources of fruit are grouped or are very abundant in a habitat, individuals travel short distances, stay close to the most productive sites, and feed intensively on fruits (Miranda 2004; Oliveira 2003; Palacios and Rodríguez 2001). Energy conservation strategies in howler monkeys are also linked to ambient temperature (Bicca-Marques and Calegaro-Marques 1998; Estrada *et al.* 1999; Prates and Bicca-Marques 2008). Howler monkeys experience both warm and cool thermal pressures (Thompson *et al.* 2014) and display thermoregulatory behaviors when exposed to extreme temperatures (Bicca-Marques and Calegaro-Marques 1998; Muhle and Bicca-Marques 2007), which allow conserving heat during periods of low ambient temperature and dissipating heat under hot conditions.

Although much progress has been made over the past two decades in describing the spatial behavior of howler monkeys (reviewed in Fortes *et al.* 2015), most studies have concentrated on assessing the effect of either ecological or social factors on spatial behavior. No studies have yet linked the use of space by howler monkeys to variation in ambient temperature. Given that spatial behavior is influenced by multiple environmental factors, a multivariate approach could favor a better understanding of this complex phenomenon, by revealing which factor, or combination of factors, is more important for each space use variable that is measured. We aimed to assess the use of space by two groups of mantled howler monkeys to advance our knowledge of the social, ecological, and physical factors that influence spatial behavior in wild primates. Specifically, we explored the relationship between the use of space and intergroup competition, food availability, and ambient temperature.

Methods

Study Site and Subjects

We conducted our study at La Flor de Catemaco (18°26′43″N, 95°02′49″W). In this ca. 100-ha tropical forest (mainly high evergreen forest), we studied two groups of mantled howler monkeys. Group 1 comprised three adult females, three adult males, and one infant, whereas group 2 included four adult females, three adult males, and three infants. We recognized all study subjects via marks that show interindividual variation, such as lighter colored spots on the hair of feet and tail, scars, or other features. In this study, we focused on adult individuals. These groups have been studied systematically since 2012, and all individuals appear to be habituated, as they ignored our presence.

Behavioral Observations

From January 2016 to March 2017, we organized observations into periods of 4 days of fieldwork per week per group. We collected data from 06:00 h to 18:00 h. We monitored two groups of howler monkeys simultaneously. To ensure agreement between the two observers (E. Ceccarelli and A. Coyohua-Fuentes), we performed interobserver reliability analyses using Cohen's κ concordance index (Cohen 1960) and found a value of κ = 0.81, indicating that data collected by the two observers were similar.

We divided each observation day into 60-min continuous focal-animal samples (Altmann 1974), distributed homogeneously through the different hours of the day among all the individuals of each group. During each focal sample, we noted the activity (resting, eating, moving, and social interactions) and marked all trees occupied by the focal animals. We located trees with a global positioning system (GPS), and classified them as feeding or nonfeeding trees. We collected a total of 1712 h of focal samples (G1: $N = 886$ h, mean ± SD = 59.1 ± 22.7 h/month; G2: $N = 826$ h, mean ± SD = 55.1 ± 18.7 h/month).

Through all-occurrence sampling (Altmann 1974), we recorded travel events, defined as each time ≥ 51% of the adult group members moved to a different tree. We considered two travel events as independent when ≥75% of the individuals performed an activity that was not traveling for a period of ≥15 min between events. We defined this criterion based on preliminary observations that showed that a 15-min interval discriminated between movement between trees within food patches and traveling. We recorded a total of 571 travel events (G1: $N = 306$, mean ± SD = 20.4 ± 9.91 events/month; G2: $N = 265$, mean ± SD = 17.7 ± 5.58 events/month). We digitized and georeferenced all marked trees as points with the geographic information system QGIS (QGIS Development Team 2014). This allowed us to calculate daily ranging distances (i.e., the sum of euclidian distances between all trees used by each group per day) and the area occupied by each study group during each month using the local convex hull method (Getz *et al.* 2007). For these calculations, we used 4354 location points, with a mean (±SD) of 145.1 ± 57.7 points/month. In addition, we calculated: travel speed (m/s), defined as the traveled distance divided by traveling time; travel rate (number of travels/h); the rate of feeding trees used by the focal animals, calculated by dividing the number of feeding trees by the number of sampling hours; and the coefficient of variation (CV = standard deviation/mean) of the distance among feeding trees.

Using all-occurrence sampling (Altmann 1974), we recorded loud calls produced by neighboring groups. We recorded a total of 333 loud calls (G1: $N = 240$, mean ± SD = 16 ± 10.75 loud calls/month; G2: $N = 93$, mean ± SD = 5.53 ± 5.37 loud calls/month). We calculated monthly rates of loud calls by nearby groups for each group based on sampling hours.

Ambient Temperature

We used ambient temperature data collected by an automatic meteorological station (Coyame, 18°26′15″N, 95°01′32″W) belonging to the Mexican National Meteorological Service located ca. 2 km from the study area. The station is at an altitude and of a habitat type similar to those of the study area. From this meteorological station, we obtained the maximum and minimum values of ambient temperature for each fieldwork day. With these data, we calculated monthly mean maximum and minimum ambient temperature.

Determination of Fruit Availability

To assess the availability of fruit, we estimated its density, distribution, and abundance (Chaves and Bicca-Marques 2016). Within the home ranges of each of the two study groups, we plotted 20 linear transects of 50 × 2 m (i.e., 2000 m^2) in which we identified to the species level all trees with diameter at breast height (DBH) ≥10 cm (Gentry 1982). We identified 128 trees from 17 different species that belonged to top food species, i.e., those that contribute 80% of the feeding time, previously reported for mantled howler monkeys in Los Tuxtlas (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). To estimate the temporal changes in the presence of fruits, we marked all identified transect trees and once a week we noted whether fruits were present using semiquantitative scores (Fournier 1978): 0 = total absence; 0.25 = presence of fruits 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 monthly mean fruit biomass per top food species with the following formula:

$$\text{Mean fruit biomass} = \text{mean Fournier score} \times \left(47 \times \text{DBH}^{1.9}\right)$$

where $47 \times \text{DBH}^{1.9}$ expresses an allometric relationship between trunk size and fruit production (Whittaker and Woodwell 1968).

We also calculated the importance index of each top food species in the home range of each group as a measure of its availability (Salomão *et al.* 2012). This index is calculated as the sum of the density (number of trees of one species/2000 m^2), frequency (number of transects in which the species was found/20 transects), and dominance (sum of the basal area of the species in the sampled 2000 m^2). We then calculated for each of the 17 top food species a monthly fruit availability index (FAI) by multiplying its monthly mean fruit biomass by its importance index (Agostini *et al.* 2010). Finally, for each month, the total FAI of the home range of each group was calculated by summing the FAI indexes of all top food species.

Data Analysis

We ran four linear mixed models (LMMs: West *et al.* 2014), one for each of the following dependent variables: area used per month, travel speed, travel rate, and daily ranging distance. We log transformed dependent variables to normalize their residuals. The independent fixed variables were group identity, maximum ambient temperature, minimum ambient temperature, FAI index, rate of loud calls by neighboring groups, rate of used feeding trees, and the CV of the distance among used feeding trees. As there is evidence that dominance relationships between neighboring mantled howler monkey groups may correlate with behavioral variation (Hopkins 2013), we also included in models the interaction between group identity and the rate of loud calls by neighboring groups. We included month identity as a random independent variable in all models to account for the repeated sampling of the two groups each month. We followed an information-theoretic approach (Burnham and Anderson 2002) to generate a set of models based on information criteria (i.e., AICc), and defined the best model for variation in each dependent variable by averaging parameter estimates of models receiving substantial empirical support (i.e., $\Delta_i < 2$). To test whether fixed independent variables were a better fit for dependent variables than random variables, after defining the best models, we used a likelihood ratio test to compare a null model including only the random factor with a full model including all fixed independent variables included in the best model (R package "stats"). We also calculated the relative importance for each independent variable included in this model set. Importance is the sum of the Akaike weights w_i of all models which include the independent variable in question. As model weights represent the probability of a model to be the best model in the model set and thus reflect model uncertainty, importance can be understood as the likelihood that a term is included in the best model. We then used function "anova" from package "car" to calculate P-values for each independent fixed factor included in the best models. Although combining information-theoretic modeling with significance testing increases the likelihood of statistical type I errors (e.g., Mundry 2011), we report results from both approaches to provide comparison (Symonds and Moussalli 2011). We examined the variance inflation factor (VIF) of the independent variables in each model to verify multicollinearity and found that none had a $\text{VIF} > 3$ (i.e., no collinear effects on other factors: Zuur *et al.* 2010). To measure the effect size of each model, we calculated the marginal determination coefficient (R^2m), which describes the proportion of the variance explained only through fixed independent variables (Nakagawa and Schielzeth 2013). All analyses were performed with R 3.3.2 (R Core Team 2017) using packages lme4 1.1–13 (Bates *et al.* 2016), car 2.1–4 (Fox and Weisberg 2016), and MuMln 1.15.6 (Barton 2016).

Data Availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Ethical Note

Our study was noninvasive and followed the Guidelines of Best Practices for Field Primatology of the International Primatological Society. Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/10637/11 and SGPA/DGVS/04999/14) and adhered to the legal requirements of Mexican law (NOM-059-SEMARNAT-2010). The authors have no conflict of interest to declare.

Results

Area used per month and travel attributes of the two groups varied considerably throughout the study (Table I). On average, group 1 used areas much larger than group 2. Moreover, whereas travel rate was the same for both groups, group 1 traveled faster and farther than group 2.

Area Used per Month

The best model to explain variation in area used per month was significantly different from the null model ($\chi^2 = 25.9$, $P < 0.001$). The best model explained 70% ($R^2\text{m} = 0.70$) of variation in area used per month (Table II). Only group identity had a significant effect, with group 1 using an area per month that was two times larger than that of group 2 (Fig. 1).

Table I Descriptive statistics for variables pertaining to the use of space by two groups of mantled howler monkeys studied at La Flor de Catemaco (Mexico) between January 2016 and March 2017

Variable[a]	Group 1			Group 2		
	Mean	SE	Range	Mean	SE	Range
Dependent						
Area used per month (ha)	6.2	4.5	0.7–19.1	3.5	3.8	0.3–14.5
Travel speed (m/s)	0.34	0.05	0.04–0.79	0.28	0.03	0.14–0.50
Travel rate (events/h)	0.33	0.03	0.15–0.60	0.33	0.02	0.23–0.56
Daily ranging distance (m)	741.0	115.6	110.3–1793.8	433.9	55.0	156.8–791.2
Independent						
Maximum ambient temperature (°C)	26.9	0.8	19.6–31.3	26.8	0.7	22.7–31.0
Minimum ambient temperature (°C)	14.9	0.8	7.7–18.9	15.2	0.6	9.7–17.7
FAI index	14.55	0.13	13.27–15.07	15.30	0.09	14.76–15.84
Rate of loud calls by neighboring groups	0.22	0.05	0.00–0.74	0.03	0.01	0.00–0.11
Rate of used feeding trees	0.40	0.05	0.12–0.84	0.39	0.04	0.12–0.80
CV of the distance among used feeding trees	0.61	0.03	0.36–0.74	0.66	0.07	0.01–1.00

[a] All statistics calculated from monthly records

Table II Model-averaged LMM of variation in area used per month in two groups of mantled howler monkeys studied in La Flor de Catemaco (Mexico) between January 2016 and March 2017

Term[a]	ß	SE	95% CI	No. of models[b]	Importance	*P*
Intercept	22.7	0.8	2.23 to 5.32	6		
Group id	−2.1	0.4	−1.60 to −0.11	6	1.00	<0.001
Rate of loud calls	3.4	5.4	−1.80 to 19.97	6	1.00	0.763
Group id × rate of loud calls	−3.6	6.1	−13.75 to 2.57	6	1.00	0.119
CV of distance among feeding trees	−2.5	0.3	−0.55 to −0.56	4	0.74	0.341
Rate of used feeding trees	2.5	0.2	−0.23 to 2.14	4	0.73	0.968
FAI index	−1.6	0.3	−0.49 to −0.28	3	0.49	0.555

[a] Predictors with significant effects are represented in bold

[b] Number of models with $\Delta_i < 2$ in which the term was included

Travel Attributes

The full models to explain variation in travel speed, travel rate and daily ranging distance were significantly different from the null models (travel speed: $\chi^2 = 8.4$, $P < 0.05$; travel rate: $\chi^2 = 27.0$, $P < 0.001$; distance traveled: $\chi^2 = 11.1$, $P < 0.05$). The best models (Table III) for travel speed and travel rate had R^2m of 0.56, and the best model for daily ranging distance had an R^2m of 0.28. Travel speed was negatively influenced by minimum ambient temperature (Fig. 2). Travel rate was significantly influenced by group identity, rate of loud calls by other groups, CV of the distance among feeding trees, and minimum ambient temperature (Fig. 3). Specifically, travel rate was higher in group 2 than group 1 (Fig. 2A), was positively related to rate of loud calls by other groups (Fig. 2B), and was negatively related to both the CV of the

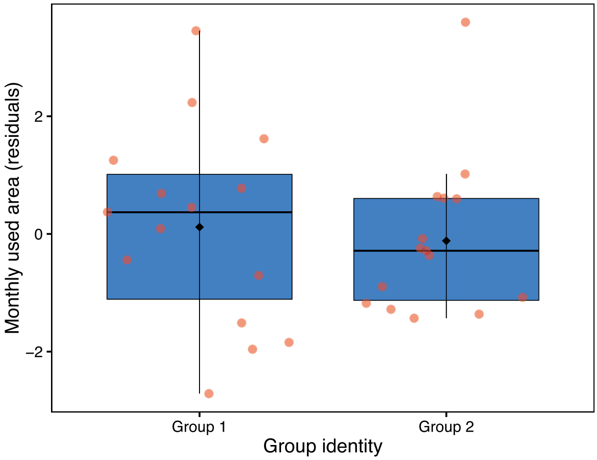

Fig. 1 Relationship between group identity and area used per month in two groups of mantled howlers in La Flor de Catemaco (Mexico), between January 2016 and March 2017. We obtained residuals from the best model excluding the variable of interest (group identity). Thick lines inside the boxes show the medians; black diamonds are the means; box limits are the 25th and 75th percentiles; the widths of the boxes represent the range; and whiskers indicate the minimum and maximum values. Data points are plotted as red circles.

Table III Model-averaged LMM of monthly variation in travel speed, travel rate, and daily ranging distance in two groups of mantled howler monkeys studied in La Flor de Catemaco (Mexico) between January 2016 and March 2017

Dependent variable	Term[a]	ß	SE	95% CI	No. of models[b]	Importance	*P*
Travel speed	Intercept	−0.06	0.66	−1.36 to 1.24	4		
	Minimum ambient temperature	−0.11	0.04	−0.18 to −0.03	1	0.29	0.005
	CV of distance among feeding trees	0.46	0.51	−0.54 to 1.45	1	0.19	0.366
	Rate of loud calls	0.46	0.58	−0.67 to 1.59	1	0.15	0.422
Travel rate	Intercept	−0.5	0.36	−1.19 to 0.23	8		
	Minimum ambient temperature	−0.1	0.01	−0.09 to −0.28	3	0.49	<0.001
	Rate of loud calls	1.8	2.27	−2.63 to 6.27	6	0.76	<0.001
	Group id	0.3	0.12	0.07 to 0.54	4	0.60	0.004
	CV of distance among trees	−0.5	0.26	−1.01 to −0.01	4	0.53	0.049
	Group id × rate of loud calls	−0.7	2.15	−4.91 to 3.53	3	0.44	0.749
Daily ranging distance	Intercept	10.6	3.2	4.30 to 17.00	3		
	FAI	−0.4	0.2	−0.86 to 0.04	2	0.51	0.076
	Group id	0.2	0.3	−0.41 to 0.82	2	0.72	0.665
	Rate of loud calls	8.9	4.4	0.24 to 17.47	2	0.72	0.900
	Group id × Rate of loud calls	−8.5	4.2	−16.83 to −0.25	2	0.72	0.043

[a] Predictors with significant effects are represented in bold

[b] Number of models with $\Delta_i < 2$ in which the term was included

distance among feeding trees (Fig. 2C) and minimum ambient temperature (Fig. 2D). Only the interaction term had a significant effect on daily ranging distances: when loud calls from neighboring groups were more frequent, daily ranging distances were longer for group 1 and shorter for group 2 (Fig. 4).

Discussion

Our results show that, whereas food availability did not influence the use of space by mantled howler monkeys, travel rate and speed were related to ambient temperature, and travel rate was also linked to the spatial distribution of feeding trees. Furthermore, loud calls by neighboring groups were influential in variation in travel rate. Studies of the spatial behavior of howler monkeys (reviewed in Fortes *et al.* 2015) and other primates (e.g., L'Hoest's monkeys [*Cercopithecus lhoesti*] and blue monkeys [*C. mitis doggetti*]: Kaplin 2001; Angolan black-and-white colobus [*Colobus angolensis ruwenzorii*]: Fashing *et al.* 2007; chimpanzees [*Pan troglodytes*]: Potts *et al.* 2016; Cat Ba langurs [*Trachypithecus poliocephalus*]: Hendershott *et al.* 2018) usually focus

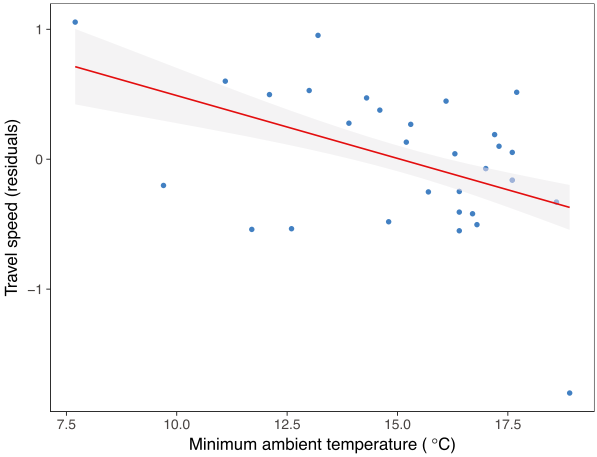

Fig. 2 Relationship between minimum monthly temperature and travel speed in two groups of mantled howlers in La Flor de Catemaco (Mexico), between January 2016 and March 2017. We obtained residuals from the best model excluding the variable of interest (minimum ambient temperature). Area shaded in gray represents the 95% confidence interval.

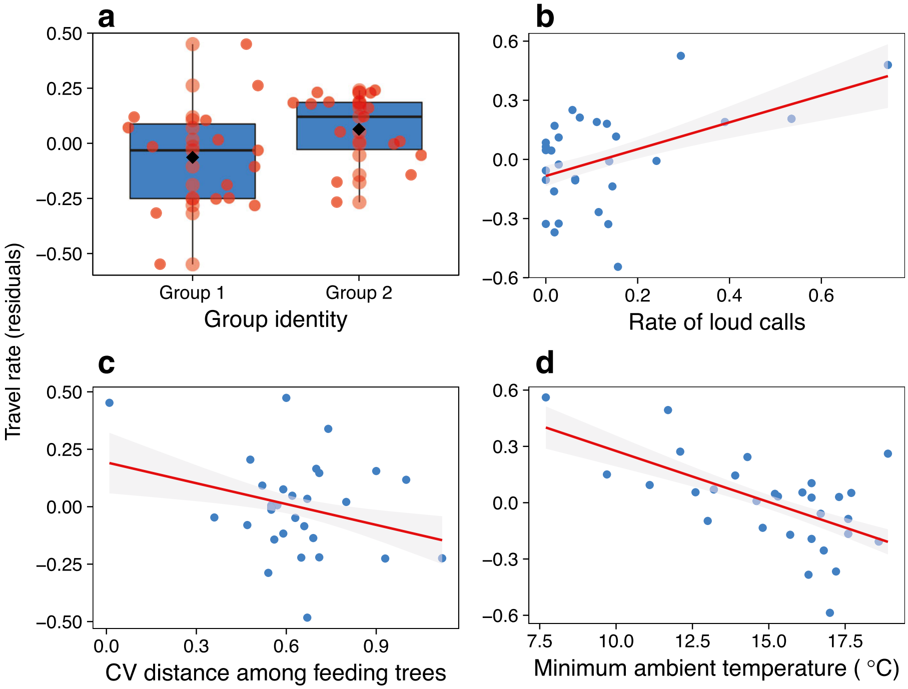

Fig. 3 Variation in monthly travel rate in two groups of mantled howlers in La Flor de Catemaco (Mexico), between January 2016 and March 2017, as a function of **(A)** group identity; **(B)** rate of loud calls by neighboring groups; **(C)** coefficient of variation (CV) of the distance among feeding trees; and **(D)** minimum ambient temperature. We obtained residuals from best models excluding the variables of interest. In **A**, thick lines inside the boxes show the medians; black diamonds are the means; box limits are the 25th and 75th percentiles; the widths of the boxes represent the range; and whiskers indicate the minimum and maximum values. In **B**, **C**, and **D** areas shaded in gray represent 95% confidence intervals.

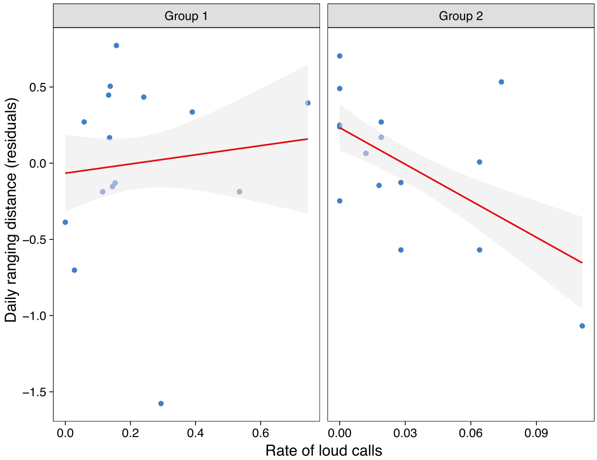

Fig. 4 Relationship between the monthly rate of loud calls by neighboring groups and daily ranging distance in two groups of mantled howlers in La Flor de Catemaco (Mexico), between January 2016 and March 2017. We obtained residuals from the best model excluding the variable of interest (i.e., the interaction between group identity and the rate of loud calls by neighboring groups). Areas shaded in gray represent 95% confidence intervals.

on the effects of either ecological or social factors, and no studies have linked the use of space by howler monkeys to variation in ambient temperature. Our multivariate exploration suggests that future studies of this topic should aim to test social, ecological, and physical factors simultaneously to better understand the spatial behavior of primates.

When exploring the influence of social factors on spatial behavior, we found that individuals moved more frequently when they heard more vocalizations, and groups differed in their response to vocalizations. Loud calls of howler monkeys convey information on spatial location and intergroup relationships (Chiarello 1995b; da Cunha and Jalles-Filho 2007; Holzmann *et al.* 2012; Whitehead 1989). By vocally announcing its location daily, a group of howler monkeys provides information that can be used by neighboring groups to track their movements over time (Chiarello 1995b; Harris 2007; Kitchen 2004). In this context, variation between groups in their spatial response to vocalizations may depend on the evaluation of the risks associated with encounters (Kitchen *et al.* 2004; Perry 1996; Treves 2001). For two neighboring groups that interact through time, varying spatial behavior associated with intergroup vocalizations may represent a defined dominance hierarchy (Hopkins 2013). Studies based on a larger sample of groups are required to assess the influence of group attributes and of the history of intergroup interactions on the spatial behavior of howler monkeys, a topic that has not been addressed to date.

Mantled howler monkeys at La Flor de Catemaco did not adjust traveling to fruit availability, suggesting that groups did not search their home ranges for fruits, as reported for other primate species (Japanese macaques [*Macaca fuscata*]: Hanya 2004). Many species (e.g., mountain gorillas [*Gorilla gorilla*]: Watts 1988; bamboo lemurs [*Hapalemur griseus*]: Overdorff *et al.* 1997), including mantled howler monkeys (Estrada *et al.* 1999), spend less time moving when the biomass of food is high, although in other species traveling time increases with increasing fruit consumption

(*Macaca fuscata*: Agetsuma and Nakagawa 1998; *Nomascus concolor jingdongensis*: Fan *et al.* 2008). Previous reports have shown that the biomass of foods preferred by mantled howler monkeys does not vary considerably throughout the year at La Flor de Catemaco (Cano-Huertes *et al.* 2017). We also found that variation in FAI index was small in both groups (CV < 4%). Furthermore, food availability is higher in La Flor de Catemaco than at other locations in Los Tuxtlas (e.g., more and bigger trees, more trees from top food species, lower primate population density: Cano-Huertes *et al.* 2017). As a consequence, it is possible that the spatial behavior of individuals living at this site is not affected by food availability. However, we also found that the spatial distribution of food resources influenced movement; the travel rate was lower when distance among feeding trees was higher, reflecting previous findings in this (e.g., Chapman 1988; Hopkins 2016) and other (e.g., *Alouatta caraya*: Bravo and Sallenave 2003) howler monkey species. Howler monkeys usually exploit a cluster of trees by moving frequently from one to another, and occasionally travel longer distances toward a new cluster farther away (Milton 1980). Therefore, food distribution may be an important factor for variation in use of space patterns, even under high availability conditions such as those at La Flor the Catemaco.

Travel speed and rate decreased with increasing ambient temperature. In contrast, the increase in ambient temperature did not influence area used per month nor ranging distances. Maintaining a constant body temperature is essential for efficient metabolism (Angilletta *et al.* 2010). When an individual is outside its thermoneutral zone, behavioral thermoregulatory strategies can help offset the energy costs of physiological regulation of body temperature (Hey 1975; Terrien *et al.* 2011). The observed reduction in locomotion under higher temperatures is consistent with the thermal constraints that explain the adoption of thermoregulatory strategies when animals are exposed to very high or very low ambient temperatures (Bicca-Marques and Calegaro-Marques 1998; Muhle and Bicca-Marques 2007). Therefore, our results suggest that the interplay of temperature and thermoregulation may represent an important selective pressure for howler monkeys.

In summary, social (i.e., loud calls), ecological (i.e., distance between feeding trees), and physical (i.e., ambient temperature) factors influence the use of space of mantled howler monkeys, although the specific effects of these factors vary among measures of spatial behavior. In addition, although the study groups were similar in size and composition, group identity was an influential factor in space use variation, suggesting that other variables, such as female reproductive state or intergroup dominance relationships, which we did not assess, may be important influences on space use. Given that studies of howler monkeys and other primates usually assess the influence of either social or ecological factors on spatial behavior, but not both, our results highlight the importance of taking a multifactorial approach to understanding primate spatial behavior.

Acknowledgements We dedicate this study to our dear colleague and friend Diana Angeles Ramirez Saldivar, who dedicated her life to study and protect wildlife in Mexico and Malaysia. 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 Ing. J. L. Ponce Puente facilitated our work in a variety of ways. We thank C. M. Schaffner for her kind review of a previous version of the manuscript. J. M. Setchell and two anonymous reviewers provided very helpful feedback and corrections on previous versions of the manuscript. This study was supported by Universidad Veracruzana and Conacyt (beca doctoral 592163; 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. A. Rangel-Negrín and P. A. D. Dias thank Mariana and Fernando for constant support and inspiration to study primate behavior.

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