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The Challenge of Coexistence: Changes in Activity Budget and Ranging Behaviour of Brown Howler Monkeys in Response to the Presence of Conspecifics and Heterospecifics

Gisela Sobral[1] · **Lisieux F. Fuzessy**[2] · **Claudio Alvarenga de Oliveira**[1]

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Abstract

The presence of other animals, both conspecifics and heterospecifics, is a major driving force for how animals organize themselves in space and time. Although theoretical models are available to explain the role of each in animal movement, fine-scale assessments of daily movement are scarce, particularly for primates. Hence, our goal was to assess whether and how the presence of conspecifics and heterospecifics influence spatiotemporal landscape use in two, wild, howler monkey (*Alouatta guariba*) groups. We followed the groups for 14 months in a large, continuous forest, during which we recorded their daily path length (DPL), home range, activity budget, feeding, and the presence of other groups (conspecifics) and other species (heterospecifics). The two groups differed in DPL, home range, proportion of fruits ingested, and time devoted to moving and resting. Partial least squares path modelling showed that variation in DPL was explained by the percentage of leaves or fruits ingested and by the presence of conspecifics, but not of heterospecifics. Group differences in several ecological variables emphasise the need to conduct further studies of space use with more groups in the same area to understand the underlying mechanisms of these differences. Moreover, our analysis shows that within-species interactions may be a stronger force in spatiotemporal organisation than interspecies interactions, at least in this folivorous primate. This is relevant from both a theoretical standpoint, and also when considering the consequences of habitat fragmentation and reduction. Deforestation leads to decreased resource availability and increased likelihood of encounters with conspecifics, which ultimately alters the proportion of food items ingested and increases the DPL, disrupting energy balance.

Keywords Activity budget · Daily path length · Home range · Interspecific interactions · Intraspecific interactions · Time budget

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Introduction

Recent advances in technology have given us a broad understanding of large and global scales of animal movement (Cooke *et al*., 2004; Nathan *et al.,* 2022). Simultaneous tracking of animals and environmental data allowed the prediction of how animals respond to environmental changes (Courbin *et al.,* 2014; Bestley *et al.,* 2015; Nathan *et al.,* 2022), how animals perceive the landscape (Janmaat *et al.,* 2021), where do animals go while migrating (Hobson *et al.,* 2019), and the requirements, avoidances, and motivations of animal movement (Nathan *et al.,* 2022). However, primates, despite being well-known for many aspects of their behaviour, many species still lack fine-scale assessment of their daily movements, particularly because many species are elusive or rare or because of the inherent challenges of data collection (Kamilar & Beaudrot, 2013; Pinto *et al.,* 2013; Sanz *et al.,* 2022).

Resource distribution is one of the main external factors that influence animal movement. While leaves are assumed to be abundant and evenly distributed, young leaves may be spatially and temporally aggregated (Agetsuma, 1995; Harris & Chapman, 2007) and ripe fruits are even more so (Milton, 1979). Energetic and chemical composition differences influence the digestion of leaves, meaning that some species prefer young leaves and soft parts over mature leaves as the former are easier to digest or rich in protein (Matsuda *et al.,* 2017). Moreover, because leaves are generally abundant and nonmonopoliseable, food competition is considered to be relaxed in folivores (Harris & Chapman, 2007; Isbell, 1991), with scramble competition for food predominating (Isbell, 1991). However, many dietary specialists (e.g., folivores) also complement their diet with other food sources (e.g., fruits) (Bonvicino, 1989; dos Santos-Barnett *et al.,* 2022; Snaith & Chapman, 2007). Hence, animals travel to find good food patches or items (Cunningham & Janson, 2007) aiming to maximize energy intake while minimizing the costs of travelling (Pyke, 2019).

Interactions with conspecifics or heterospecifics also influence animal movement. Animals may move in response to physical (Sanz *et al.,* 2022), visual (Markham *et al.,* 2012; Bonadonna *et al*., 2020) and acoustic cues and signals (Kurihara & Muto, 2021; Van Belle & Estrada, 2020) from other individuals, other groups, or other species. Although some species benefit from mixed-species aggregations to avoid predators or to increase foraging efficiency (e.g., mixed-species troops of callitrichine primates: Heymann & Buchanan-Smith, 2000), other interactions between individuals or between species may be adverse. Adverse interactions comprise the well-known predator-prey relationship (Di Bitetti *et al.,* 2009; Schoener, 1974; Sih, 2005; Singh *et al.,* 2000) or foraging competition. Food competition is a major cost of group living among social animals (Janson, 1985) and can also occur between sympatric species (Sobroza *et al.,* 2021). Individuals or species that compete frequently may have to forage for longer or travel further (Harris & Chapman, 2007; Isbell, 1991; Janson & Van Schaik, 1988).

Howler monkeys (genus *Alouatta*) are an excellent model for addressing the influence of intra- and interspecific interactions on movement. Many howler populations live at high densities (Chiarello, 1992; Bravo & Sallenave, 2003; Kowalewski, 2007; Goméz-Posada & Londoño, 2012), and they may increase their daily range in response to intergroup encounters (Agostini *et al.,* 2010a; Ceccarelli *et al.,* 2019; Raño *et al.,* 2016). The genus is characterised by intragroup scramble competition for food (Behie *et al.,* 2010; Isbell, 1991). Such scramble competition is difficult to measure so measures of spatiotemporal use of the landscape, such as daily path length (DPL) and moving/feeding time, often are used as proxies (Isbell, 1991; Raño *et al.,* 2016). To reduce competition, animals may increase either feeding time or their daily travel movements (Harris & Chapman, 2007; Isbell, 1991; Janson & Van Schaik, 1988). For instance, DPL increases in response to a greater proportion of mature fruits ingested or decreasing with a greater proportion of mature leaves ingested (Raño *et al.,* 2016). In contrast, similar values in DPL and activity budget among groups may indicate similar levels of competition or similar habitat quality (Jung *et al.,* 2015; Schreier *et al.,* 2021), whereas the presence of heterospecifics does not necessarily influence DPL due to other mechanisms, such as niche partitioning as observed among sympatric strepsirrhines (Bersacola *et al.,* 2015).

Howler monkeys also have a wide geographic range (Cortés-Ortiz *et al.,* 2003), frequently overlapping in distribution with other primate species (Cristóbal-Azkarate *et al.,* 2015). A series of studies of two sympatric howler species found no evidence that interspecific interaction influenced daily range (Agostini *et al.,* 2010a, 2010b; Agostini *et al.,* 2012). Other studies addressing heterospecific interactions show that these interactions can include physical aggression (e.g., capuchins, Falótico *et al.,* 2021) or in howlers being chased or result in displacing howlers from their feeding trees (Mendes, 1989; Dias & Strier, 2000; Rose *et al*., 2003; Martins, 2008), potentially influencing their DPL.

Brown howler monkeys (*Alouatta guariba*) are one of the 25 most threatened primate species in the world (Buss *et al.,* 2019; Oklander *et al.,* 2022) following a yellow-fever outbreak, which increased their threat level from Least Concern to Vulnerable (Jerusalinsky *et al.,* 2020). Our focal population in Carlos Botelho State Park (PECB), São Paulo, Brazil, is a low-density population (González-Solís *et al.,* 2001), which inhabits one of the few, large, continuous, protected remnants of the Atlantic Forest (approx. 38,000 ha) (Rosa *et al.,* 2021). These two characteristics are unlike the majority of studies conducted with *Alouatta*, because most studies have been conducted with high-density populations (Chiarello, 1992; Bravo & Sallenave, 2003; Kowalewski, 2007; Goméz-Posada & Londoño, 2012) inhabiting small, fragmented, and altered landscapes (Chaves *et al.,* 2019). Studies of activity budget and space use conducted in these small fragments may not show the full extent of variation in this species. Moreover, PECB howlers live in sympatry with two primate species: the southern muriqui (*Brachyteles arachnoides*) and the capuchin monkey (*Sapajus nigritus*). All three species consume local fruits (*B. arachnoides*: Carvalho Jr. *et al*., 2004; *S. nigritus*: Izar *et al.,* 2012), a food resource of high-energetic value and important in food competition (Caillaud *et al.,* 2010; Chapman, 1990; Chapman *et al.,* 1995; Strier, 1989). In terms of habitat quality, reduction in forest size has several direct and indirect implications for species' movement. The cascade of consequences include increased travel distances, blocked migration, increased population density, reduced resource availability, and increased competition (Knowlton & Graham, 2010).

We tested the hypothesis that changes in activity budget and DPL in these howlers will be due to the presence of conspecifics or heterospecifics. If this is the case, then we predict that groups will move further and for a longer time when encounters are more frequent.

Methods

Study Area

We conducted our study in Carlos Botelho State Park (PECB), São Paulo, Brazil. The park is approximately 38,000 ha. Together with other public and private-owned parks, it forms part of the Serra de Paranapiacaba Ecological Continuum, an area of some 250,000 ha of Atlantic Forest, and one of the largest surviving remnants of this highly-threatened domain (Pisciotta, 2002; Ribeiro *et al.,* 2009).

The park is considered a nonseasonal ecosystem in terms of rainfall and temperature but has marked fruiting seasons (Morellato *et al.,* 2000). Rainfall at the study site is more abundant in the summer, with lower amounts during winter, without a real dry period (Plano de Manejo, 2015). The mean annual temperature varies between 15 °C in winter and 24 °C in summer, with the lowest temperature (1.8 °C) recorded in July and the highest (35 °C) in December (Instituto Nacional de Meteorologia, INMET, data). Elevation varies between 700 and 850 m a.s.l., and the entire study area is in mountainous terrain where the hilltops are composed of montane and altimontane dense vegetation and lowlands are composed of ombrophilous forest (Plano de Manejo, 2015).

Study Groups

In the study region, we identified six groups individually based on their unique characteristics, such as face shape, natural markings, scars, and depigmentation. We monitored two of these groups (G3 and G4) between November 2017 and December 2018. We monitored G1 for 17 days during March, November, and December 2017. We followed a fourth group (G6) for one full day and counted individuals and recorded GPS location whenever we saw other groups.

We followed G3 and G4 between dawn and sunset for 4 to 6 days per month (1,361 h of total observation, 640 h for G3, 570 h for G4, 141 h for G1, and 10 h for G6). We provide data from 52 full-day follows for G3 and 48 full-day follows for G4, disregarding partial day-follows.

G3 and G4 were of similar size and composition. G3 was composed of one adult male, two adult females (one with a dependent infant), and two subadult males of unknown kinship. G4 was composed of one adult male, two adult females, and their offspring and one subadult male of unknown kinship. Moreover, G3 inhabited an area at the park boundary and its movement was limited by open grasslands, roads, and houses. Canopy was either naturally connected or artificially connected with canopy bridges. G3 lived close to the park headquarters and had daily contact with humans. Conversely, G4 occupied an area approximately 3 km from the headquarters, accessible only to researchers.

Home Range and Daily Path Length

While we followed the groups, a GPS collected 260 location records per day. From these points, we selected a subset of locations every 20 minutes if the groups were moving or once an hour if the groups were resting, because they could spend several hours without moving. Whenever we detected nontarget groups, we took the GPS location and identified individuals. We used these points to create a home-range map for each group, connecting the outermost GPS points with QGIS. Hence, we created polygons for graphic representation (Fig. 3), but this does not represent their true home range.

Using the GPS points, we calculated DPL by summing the linear distances between the GPS interval points (Raño *et al.,* 2016). We also stimated home range (95%) and core area (50%) for G3 and G4 based on Minimum Convex Polygon method (MCP, Worton, 1995) and the Kernel Density Estimate (KDE, Powell, 2000; Kernohan *et al.,* 2001). For KDE, we used an *ad hoc* method for choosing the smoothing parameter ("href"), with metres as the unit in and hectares (ha) as the unit out. We provide both estimates to allow for comparison with previous works, which used MCP only while also providing the most widely used home-range estimation methods, KDE. We calculated areas with the *mcp.area* and *kernelUD* functions in the adeHabitatHR package (R Core Team, 2019). Although we have enough data to calculate G1's home range, two individuals were not habituated, potentially altering group behaviour and their DPL so opted to not include this group in our study. However, because we followed G1, G3, and G4 consistently, we are confident enough to state whether two or more groups shared the same areas. We considered home ranges to overlap if two or more groups shared some GPS locations, that is, if we observed two or more groups in the same areas.

Activity Budget

We calculated the activity budget for G3 and G4 using scan sampling (Altmann, 1974). Every 20 minutes, we recorded the following categories for each individual during a 2-min window: foraging (feeding, manipulating, and ingesting food or drinking water), moving (movement in any direction and speed), resting (immobile or sleeping), socialising (play, grooming, and any other social interactions between individuals), and others (any behaviour that did not fit within these categories). We summed all cases in which visible individuals were involved in a given behaviour and divided this by the number of individuals visible to obtain the proportion of each behaviour during the scan sample. Then, we took the mean of the proportions for each scan sample for the whole day to obtain daily proportions of each behaviour and monthly proportions of each behaviour. The groups were small and cohesive, so it was unlikely that we missed an individual in a scan. In total, we recorded 3,656 individual activities for G3 and 4,656 for G4.

Feeding Bouts

To understand whether the presence of conspecifics or heterospecifics influenced the amount of leaves and fruits ingested, we recorded a feeding bout whenever more than 50% of scanned individuals were foraging during a scan sample, identified the plant part consumed (if possible), and recorded the GPS location, similar to Bryson-Morrison *et al.* (2017) and Back & Bicca-Marques (2019). We then calculated daily percentages of fruits or leaves consumed, including records when we could not identify the food item in the total.

Presence of Conspecifics or Heterospecifics

Because the muriquis and capuchins have been studied over the past 20 years, many howler monkey groups are habituated to human presence, allowing us to witness interspecific encounters in detail. We recorded audible loud calls emitted both by neighbouring groups and by the group we were following. We considered howling bouts independent when calling had ceased for ten consecutive minutes between two calling bouts (Van Belle *et al.,* 2013). Loud calls could occur during intergroup encounters, (i.e., when two groups saw each other). We recorded the presence of conspecifics daily, including both audible vocalisation bouts and visual intergroup encounters.

We used the same rationale for the presence of heterospecifics, including both audible vocalizations and visual encounters of other species. There are no standard methods for recording interspecific encounters (Falótico *et al.,* 2021), so we recorded heterospecific encounters as events, regardless of the number of individuals involved, and the duration of the interaction (Scarry, 2013). Encounters with the same species on the same day were rare, usually occurring between 30 minutes and 2 hours apart. We considered each encounter as an independent event and identified the outcome for howler monkeys.

Rainfall, Temperature, and Season

We obtained daily rainfall data from the park pluviometric database made available to us by the manager. The National Institute of Meteorology (INMET) provided hourly temperature data. Because the region does not have a dry period, we divided the seasons by combining water surplus (Walter, 1973) and peak fruit availability (Talebi *et al.,* 2005). A water surplus occurs when the rainfall exceeds twice the mean maximum temperature in degrees Celsius (20.4 °C). Thus, we considered the period between October and March as the wet-nonfruiting season and April to September as the dry-fruiting season (Fig. 1).

Statistical Analysis

We tested data for normality and, because it was nonnormally distributed, we used Kruskal Wallis tests with Dunn *a posteriori* tests to test for differences between groups in home range, DPL, and percentages in each activity budget behaviour.

To evaluate the direct and indirect effects of season, group identity (group ID), activity budget, feeding bouts, and presence of heterospecifics and conspecifics on DPL, we used partial least squares path modelling (PLS) based on the plspm package (Sanchez, 2013) in the R software (R Core Team, 2019). Our dataset for these analyses consisted of 90 daily values. We converted season into factors, with 1 being wet-nonfruiting and 2 being dry-fruiting. We used the DHARMa package (Hartig, 2017) to test the model's residual distribution and assessed the variance inflation factor (VIF) to test for model inflation. All VIF values were <5. Because the activity budget behaviours were highly correlated among each other as well as with the consumption of leaves and fruits (assessed via ggpairs package in R), we included only resting and the percentage of fruits or leaves ingested during the feeding bouts in our model.

We built two models: one with the percentage of feeding bouts where fruits were ingested (fruit model), and one for leaves (leaf model) (Fig. 2a). Specifically, 0 means no influence and 1 means that we expect an effect from the row above to the row below (Fig. 2b). Given expected direction of effects, season cannot influence group ID, so the effect is 0. However, season can influence the presence of conspecifics and heterospecifics, activity (moving, feeding, or resting), and resource availability (leaves or fruits), so we assigned 1 to each of these. Because we detected differences across groups in the presence of heterospecifics and conspecifics, we expected that group ID would influence these variables and assigned 1 to these relationships. Finally, because our initial hypothesis was that season, group ID, activity budget, feeding bouts, and presence of heterospecifics and conspecifics influence DPL, the bottom row is composed of ones (Fig. 2b). We counted encounters with each species separately, but they were analysed together into a single block called "presence of heterospecifics." The combination of variables into blocks is a requirement for package use (Sanchez, 2013) without inflating the model. We based effect estimation on 200 bootstraps resampling and the explanatory power of the models

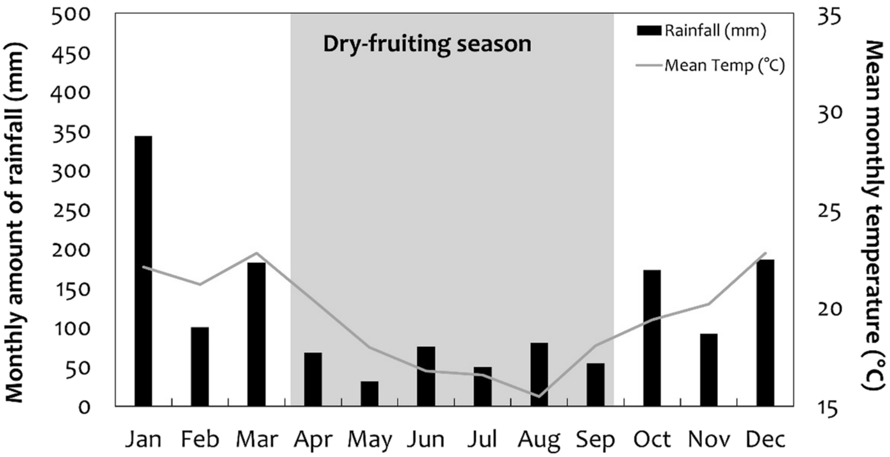
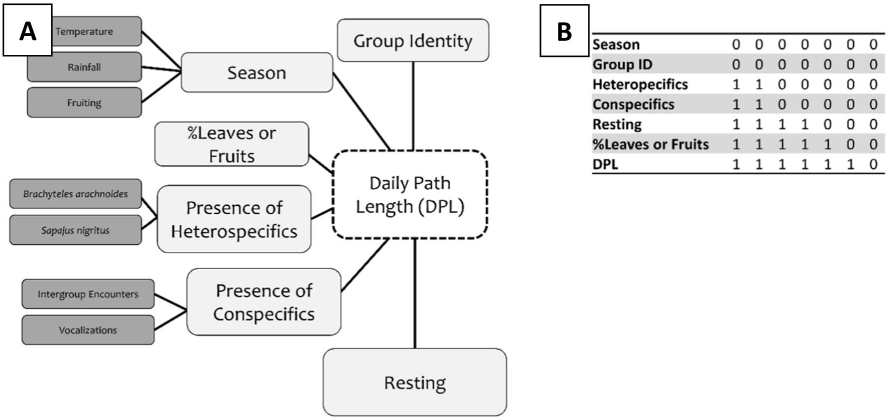


Fig. 1 Graph showing the accumulated rainfall (black bars, mm) and the mean monthly temperature (grey line, °C) for each month of 2018, in Carlos Botelho State Park (PECB), São Paulo, Brazil, combined with fruiting and non-fruiting season according to Talebi *et al.* (2005).



Season	0	0	0	0	0	0	0
Group ID	0	0	0	0	0	0	0
Heteropecifics	1	1	0	0	0	0	0
Conspecifics	1	1	0	0	0	0	0
Resting	1	1	1	1	0	0	0
%Leaves or Fruits	1	1	1	1	1	0	0
DPL	1	1	1	1	1	1	0

Fig. 2 **a** Path diagram depicting our model tested with partial least square modelling (path analysis) to assess the effects of these variables on daily path length (DPL) for brown howler monkeys (*Alouatta guariba*) in Carlos Botelho State Park (PECB), São Paulo, Brazil, between 2017 and 2018. Dark grey boxes are the variables, light grey boxes are the blocks, and white dashed box is the assessed variable. **b** Expected direction of effects. We included the percentage of leaves or fruits recorded in feeding scans separately in each model. Zero predicts no influence of a row on the row below and 1 predicts an influence of a row on the row below. Group ID: group identity. % Leaves or Fruits: percentage of feeding bouts in which leaves or fruits were the food item being consumed. DPL: daily path length.

is provided by the Goodness of Fit (GoF). All statistical analyses used software R v.4.0.3. We considered $p < 0.05$ as significant.

Ethical Note

This research was approved by the Ethics Committee on Animal Use of the School of Veterinary Medicine and Animal Science (University of São Paulo), under protocol number 4864040618. We have no conflicts of interest to declare.

Data Availability Made available under reasonable request.

Results

Group Differences in Space Use and Activity Budget

Howlers were exclusively arboreal, except for a single day on which we recorded one group using the forest floor to escape from an intergroup encounter that happened at their home range border. We never saw two groups using the same area. Mean DPL was significantly shorter for G3 than for G4 (Table I). G3's home range and core home range were much smaller than those of G4 (Fig. 3; Table I). The 95% Kernel estimate was larger than that using MCP.

In terms of activity budget, howler monkeys spent most of their time resting (53.3%), followed by foraging (22.5%), moving (13.7%), social (4.6%), and other behaviours (4.5%). However, only moving and resting were statistically different between groups (Table I).

We recorded 1,234 feeding bouts (548 for G3 and 686 for G4), and recorded the item eaten for 70% (864) of bouts (73%, $n = 401$ for G3 and 67%, $n = 463$ for G4) (Table I). Leaves were more commonly consumed than fruits in G3, but not G4. We also recorded occasional feeding on flowers ($n = 2$ feeding bouts) and gum ($n = 7$), and we observed howlers drinking water ($n = 17$) from bromeliads and tree holes.

Presence of Conspecifics and Heterospecifics

We recorded only eight intergroup encounters but 116 neighbouring group vocalisations (total 124), with a rate of 1.17 calls per day. Vocalizations heard from neighbouring groups were similar for the two groups (20 for G3 and 22 for G4), although

Table I Daily path length, home range, activity budget, and proportion of specific food items consumed by two, wild, brown, howler monkey (*Alouatta guariba*) groups in Carlos Botelho State Park, Brazil, between November 2017 and December 2018. We tested for differences between groups with Kruskal-Wallis and Dunn *post hoc* test for nonparametric variables and ANOVA and Tukey HSD *post hoc* test for parametric variables

Parameters	G3	G4	*F*	df	*p*
Mean group size (range)	6.5 (5-7)	5.5 (5-6)			
Daily path length (m)					
Mean	665	779	42.99	1, 114	<0.001
Minimum	226.5	209.0	-		-
Maximum	1198.2	2592.6	-		-
Home range (ha)					
95% Maximum Convex Polygon	15.0	41.3	22.87	1, 18	<0.001
95% Kernel	18.4	43.8			
50% Kernel (core area)	5.9	13.0			
Activity budget					
% Resting	57.2	49.4	10.29	1, 76	<0.001
% Foraging	22.3	22.6	2.46	1, 76	0.121
% Moving	9.8	17.6	14.12	1, 76	<0.001
% Other	9.2	8.9	0.251	1, 76	0.61
% Unidentified	1.5	1.6	-		-
Feeding bouts					
% Leaves	35.2	43.9	6.41	1, 79	0.01
% Fruits	36.5	21.0	0.426	1, 79	0.516
% Water	0.9	1.7	-		-
% Flower	0.2	0.1	-		
% Gum	0.4	0.7	-		-
% Unidentified	26.8	32.5	-		-

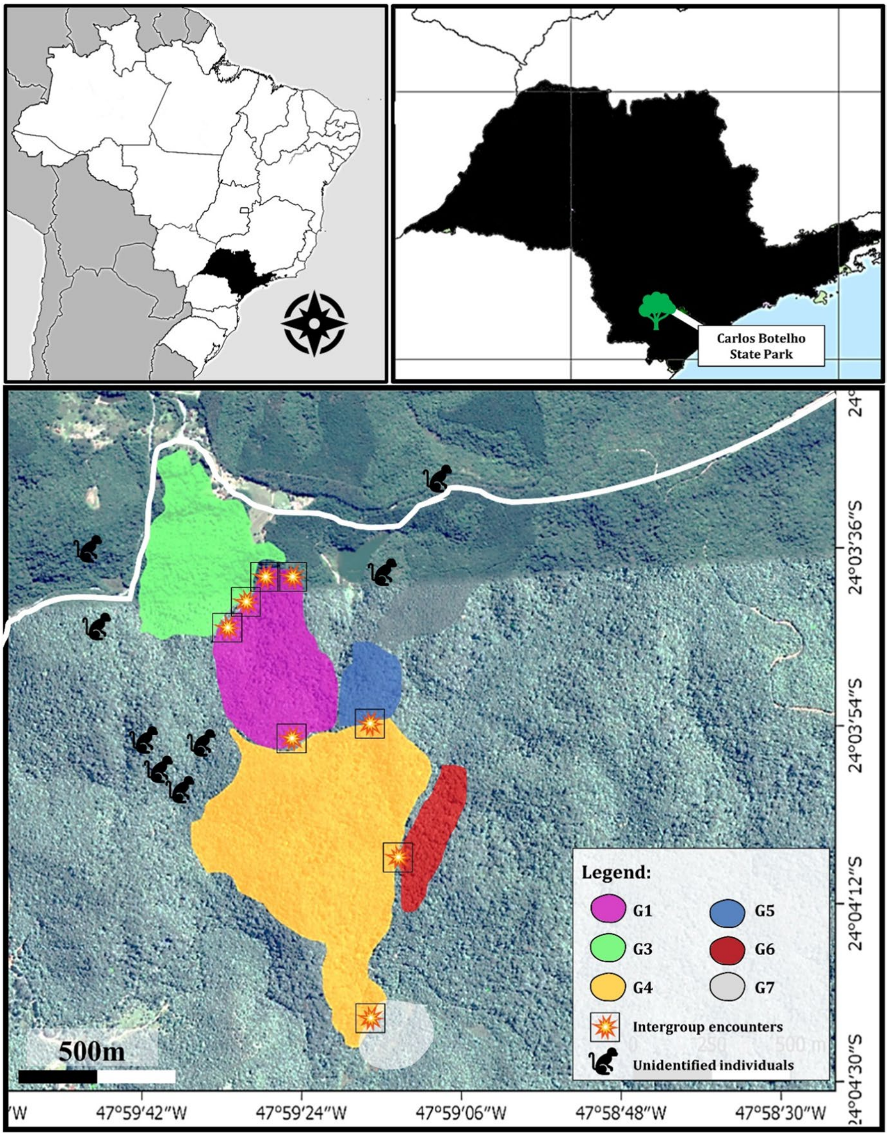


Fig. 3 Park location and home range maps of the six brown howler monkey (*Alouatta guariba*) groups known to live in Carlos Botelho State Park, Brazil, between 2017 and 2019. Colors show each group's home range. Polygons for G3 (green) and G4 (orange) were estimated based on 14 months of survey (15.0 ha and 41.3 ha, respectively). Home ranges for other groups do not represent exact values. White bold line shows the park edge. Explosion symbols show intergroup encounters. Monkey symbols show individuals that we saw but could not identify or assign to any of the known groups.

G3 howled more than G4 ($n = 57$ and 17, respectively). Considering the number of full-day follows, the rate of intergroup interactions per day were 0.38 for G3 and 0.47 for G4.

We recorded 63 encounters with other species, with muriquis ($n = 45$) being encountered more frequently than capuchins ($n = 18$). Combined, these two species were present 0.63 times per day. During visual encounters, howlers were chased 22 times, remained alert 9 times, escaped with no signs of chase 15 times, did not change their behaviour in 16, and escalated to physical interactions in three. They encountered the two other species simultaneously twice. The maximum presence recorded per day was three for each species. Of these, we could relate 50 heterospecific and 59 conspecifics to a GPS track and included these encounters in the path analysis.

Path Analysis

Our leaf model explained 43% of the variation in DPL (Fig. 4b). Group ID influenced the number of records for heterospecifics, resting, proportion of feeding bouts in which leaves were ingested and DPL. Season had a negative influence on the percentage of leaves consumed in feeding bouts (fewer leaves ingested in the dry-fruiting season). Season also had a negative effect on DPL (shorter distance travelled during the dry-fruiting season), the presence of heterospecifics recorded (fewer records during the dry-fruiting season), and the presence of conspecifics (fewer records during the dry-fruiting season). The percentage of leaves ingested also positively impacted DPL. Finally, the presence of conspecifics had a positive influence on the percentage of feeding bouts, including leaves and on the DPL. The presence of heterospecifics was not a significant explanator of DPL.

In the fruit model, explanatory power was smaller (37%). The significant effects and directions were similar to those of the leaf model (Fig. 4a and b). However, season had an opposite influence on fruits than on leaves (more fruits in the dry-fruiting

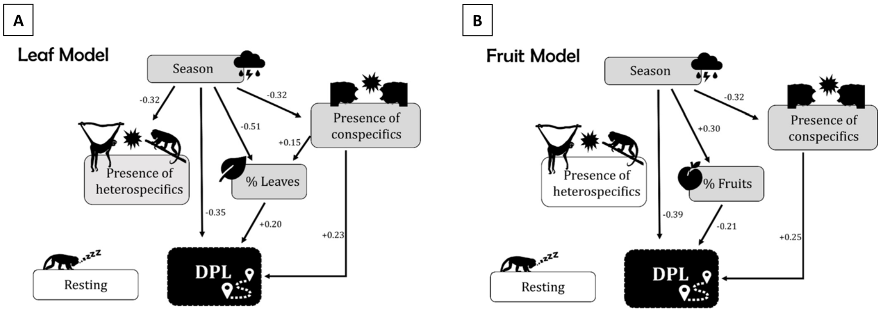


Fig. 4 Representative scheme of a leaf model (**a**) and fruit model (**b**) of two groups of brown howler monkeys (*Alouatta guariba*) in Carlos Botelho State Park, São Paulo, Brazil, between 2017 and 2018. Figures show the direct and significant effects obtained via partial least square analysis of daily path length (DPL). We based effect estimation on 200 bootstraps resampling. The model explained 43% of the variation in DPL. Black boxes show the variable assessed (DPL), grey boxes are the blocks included in the model and white boxes are variables that did not have significant relationships with any other variables.

season). The most striking difference between the two modes was the negative influence of the percentage of fruits on DPL (the more fruits ingested, the shorter the DPL). The presence of heterospecifics was not significant in explaining DPL.

Discussion

Our results partially support our hypothesis as the presence of conspecifics did alter daily movement, but the presence of other species did not. Space use varied widely between the two main study groups, and although we cannot draw strong conclusions based on this comparison, we discuss some group differences below.

Home Range

G3's home range falls within the size typically reported for the genus (average 22 ha for several howler monkey species; Fortes *et al.,* 2015), whereas G4 showed one of the highest values ever reported for the genus (exceptions include two *A. guariba* groups from Argentina, with home ranges varying between 47.4 ha and 70.3 ha; Agostini, 2009). One-third of studies of *Alouatta guariba* have been conducted in fragments smaller than the home range found in the present work (Bicca-Marques, 2003; Fortes *et al.,* 2015).

Varying home range sizes, as observed in our study, are common in primates (e.g., Cercopithecinae, Gibson & Koenig, 2012; Sha & Hanya, 2013; other Platyrrhini, Alba-Mejia *et al.,* 2013). Explanations for such differences include group size, predation risk, food resources, and neighbouring groups (Fortes *et al.,* 2015). Our groups did not vary in size. We did not assess predation risk, although we witnessed distress in response to raptors (mantled hawk *Pseudastur polionotus*) in G4 twice. We also did not analyse habitat quality or record phenology. However, food resources likely differ between the two groups' home ranges. G3's home range seems to have more fruit trees than that of G4, a suggestion that is supported by the data showing that G3 consumed more fruits than G4. The home ranges of the two groups also differed in landscape features, with G3 home range restricted by the forest edge and open grasslands, and composed of secondary forest, a habitat known for its lower quality (Ries & Sisk, 2004). Moreover, G4's home range had more hilly areas, which could also affect its quality (Jung *et al.,* 2015). Hence, G4's home range may be both larger and lower quality. However, because we lack key data to clearly understand the factors underlying the difference in home range, this remains an open question.

The presence of neighbouring groups may also influence home range size. Although we recorded similar frequencies of vocalization from neighbouring groups for both focal groups, G3 vocalized three times more than G4. Moreover, encounters between neighbouring groups were rare, and there was no overlap in home ranges between any adjacent groups. These findings indicate that PECB howler monkeys might be territorial (Powell, 2000), a definition not regularly applied to howler monkeys due to the recurrent broad overlap between neighbouring groups (Cornick &

Markowitz, 2002). The broad overlap frequently observed for the genus may be related to the small fragments in which they were studied, preventing groups from avoiding each other and leading to a large overlap in home ranges (Knowlton & Graham, 2010).

The presence of heterospecifics is not commonly reported as a mechanism influencing home range but spatial avoidance/segregation among sympatric species is a frequent outcome of interspecific competition (Houle *et al.,* 2010). G4 had 2.5 times more encounters with other species than G3. Subordinate species, as seems to be the case of howlers (see below), usually avoid dominant ones (Creel & Creel, 1995). We need more spatial distribution estimates from multiple groups to assess whether spatial avoidance/segregation in response to conspecifics and heterospecifics influences home range.

Activity Budget and Feeding

The howlers activity budget matches those reported in the literature: howler monkeys spend a large proportion of their daytime resting (45-65% for *A. guariba*, Agostini *et al.,* 2010a; Jung *et al.,* 2015; Ferreguetti *et al.,* 2020; or 64.7% for *A. caraya*, Rímoli *et al.,* 2012). The large time spent resting is proposed as an energy optimisation strategy, because leaves provide a low energetic reward (Di Fiore *et al.,* 2011; Milton, 1998). Moreover, mature leaves and unripe fruits are difficult to digest (Amato *et al.,* 2015), requiring longer digestion time (Rosenberger & Strier, 1989) and consequently, a greater amount of time devoted to resting.

The two groups differed significantly in their activity budget, with G3 resting more and G4 moving more. Differences in locomotor behaviour (such as moving) can reflect distinct habitat structures (Prates & Bicca-Marques, 2008) or distinct levels of scramble competition (Clutton-Brock *et al.,* 1997; Clutton-Brock & Harvey, 1977; Isbell, 1991). We also witnessed more aggression in G3 than in G4 (unpublished data). Given these differences, it is possible that G3 faces more contest competition (Isbell, 1991; Vogel & Janson, 2007), whereas G4 faces more scramble-like competition.

PECB howlers spent more feeding bouts eating leaves than fruits, a pattern already described for this folivorous primate (Agostini *et al.,* 2010b; Miranda & Passos, 2004). Changing from a highly folivorous to a highly frugivorous diet is one explanation for why howlers are resistant to habitat fragmentation and reduction (Bicca-Marques, 2003; Bicca-Marques *et al.,* 2020). Other primate species in PECB, such as the muriquis, tend to be more frugivorous than conspecifics inhabiting more fragmented forests (Carvalho Jr. *et al.,* 2004; Talebi *et al.,* 2005). We also found marked differences between groups in the proportion of leaves and fruits ingested, and we suggest future studies investigate these differences between neighbouring groups in a large continuous forest.

Daily Path Length

We found that G4 group not only spent more time moving but also moved greater distances. Such differences in ranging patterns between groups are important proxies for food competition (Clutton-Brock & Harvey, 1977; Isbell, 1991), meaning that G4 is potentially facing greater food competition compared to G3. Greater food competition is commonly found in larger group sizes (Isbell, 1991). However, both groups were the same size, so the observed variation in DPL can derive not from intragroup competition, but from intergroup competition or habitat qualities and resourced availability.

Overall mean DPL values were similar to those of other brown howler populations (Agostini *et al.,* 2010a; Fortes *et al.,* 2015). DPL is not very variable in *Alouatta* and seems to be independent of fragment size (Bicca-Marques, 2003). Colobus monkeys, an even more folivorous primate genus than howler monkeys, has a DPL that barely exceeds 450 m (Dasilva, 1992; Teichroeb & Sicotte, 2009). Highly folivorous animals show strategies to optimise digestion, either by reducing their activity time or their daily path length (Hladik, 1978).

Path analysis detected the influence of eating leaves and fruits on DPL, although these variables acted in opposite ways, with fruits negatively influencing DPL and leaves positively influencing it. This contrast may result from leaves requiring longer processing times than fruits, reducing DPL (Aristizabal *et al.,* 2016; Nagy & Milton, 1979; Reynoso-Cruz *et al.,* 2016). Similarly, large fruit patches may result in animals staying at those trees, without needing to travel further distances to find other patches (Jung *et al.,* 2015; Strier, 1987). Considering that G3's home range is influenced by edge effect, we can expect differences in habitat quality and structure (Ries & Sisk, 2004). Edge effects decrease the number of tree species and alter tree community composition (Benítez-Malvido & Martínez-Ramos, 2003). Larger trees with greater amounts of fruits and leaves are more common in forest interiors than at the edge (Chapman *et al.,* 1992). Although edge effects may reduce the absolute number of fruits produced because large trees are absent, young leaves that are of high nutritional value and easy to digest are more common (Arroyo-Rodríguez & Mandujano, 2006). This trade-off seems interesting for a species like howler monkeys (Bolt *et al.,* 2021) and might apply to G3, but further studies evaluating habitat quality and diet are needed in this population. If available food has a lower energetic return or is in smaller quantity, primates may reduce their daily range (energy minimizing strategy; Milton, 1980) or increase their daily range in search of higher quality food items (energy maximizing strategy; Terborgh, 2014).

Presence of Conspecifics

We recorded 116 calls during our study, with a rate of 1.17 calls per day, whereas intraspecific encounter rates were low (*n* = 8 in 100 days). Intergroup encounter rates were much lower in PECB population than reported for *Alouatta pigra* (neighbours meet once every 3 days; Van Belle *et al.,* 2013) or *A. caraya* (5.7 encounters per hour; Kowalewski, 2007), the species with the highest encounter rates reported. One study found a high correlation between roaring sessions and intergroup encounters in our study species (Cunha & Jalles-Filho, 2007). Although visual encounters were rare, path analysis suggested that these calls were enough to cause variation in DPL.

Vocalisation is a striking feature of howler monkeys, with many species showing a “morning choir” (e.g., *Alouatta seniculus*, Sekulic, 1982). Resource defence is the most strongly supported hypothesis to explain such behaviour (de Cunha *et al.,* 2015; Kitchen *et al.,* 2015). We did not observe morning or dawn chorus in the PECB howlers, although we followed from before dusk and after dawn to ensure that animals were no longer moving. This routine also required us to use a thermal sensor to detect animals at pitch-black night, even detecting some nocturnal behaviour in this population, but never howling bouts (Sobral *et al.,* 2022). Additionally, most of G3’s territory was near the dorms we slept in, so we would have heard calls if they happened.

G4 had several neighbours, unlike G3, and the presence of a greater number of neighbouring groups has the potential to increase scramble competition (Müller & Manser, 2007). However, G4 vocalised less than G3. Reduced aggression has also been observed among neighbours, the so-called “dear enemy effect” (Temeles, 1994). The population density at PECB appears to be lower than in other sites, and previous surveys did not find howler monkeys (González-Solís *et al.,* 2001). We could not easily find groups during our study (even leading to an unsampled month). However, our population’s average group size and home range (six individuals in 31 ha) suggests a density of 1.86 ind/km^2. This value is much lower than that found in island populations of *A. guariba* (1 group/km^2, Ferreguetti *et al.,* 2020) or southern South America (10 ind/km^2, Agostini *et al.,* 2010a). Given that local population density is low, intergroup encounters were rare and that home range overlap was minimal, we conclude that vocalizations alone can significantly influence DPL.

Presence of Heterospecifics

PECB howlers coexist with muriquis, large folivore-frugivore primates (Carvalho Jr. *et al.,* 2004; Talebi *et al.,* 2005) and black capuchins, medium-sized primates that feed on insects, leaves and fruits (Izar *et al.,* 2012). Encounters with other species were common, particularly for the group from the forest interior (G4) and interactions with muriquis were more common than with black capuchins. Encounter rates per day (0.63/day) are still lower than encounters between neighbouring groups of any *Alouatta* population (Cunha & Jalles-Filho, 2007; Kowalewski, 2007; Van Belle *et al.,* 2013).

In 75% of heterospecific encounters, the behaviour of howlers was disrupted by being displaced from their feeding/sleeping site, remaining alert or chasing. On three occasions, interactions became physical, including one long event with a muriqui group, although muriquis are called a friendly primate (Gross, 2017). PECB howlers never won (Cristóbal-Azkarate *et al.,* 2015) these interactions, and both capuchins and muriquis seem to be dominant over howlers. Dominant species may limit the population growth of subordinate species (Rowley & Christian, 1976). Although howlers are considered specialized folivores, fruits are their preferred food (Behie & Pavelka, 2015). Encounters with syntopic species commonly derive from—or result in—competition for food, leading to reduced fitness for competitors, especially for losers (Janson, 1985; Pruetz & Isbell, 2000). Despite this disruption, path analysis did not detect the influence of heterospecific presence on DPL, supporting the pattern observed in earlier studies (Agostini *et al.,* 2010a, 2010b, 2012).

Our analyses show the intricate effect of conspecifics and heterospecifics on ranging behaviour. Species interactions—and groups—vary in space and time (Laundré *et al.,* 2010; Prugh *et al.,* 2019). These interactions influence foraging success, with profound fitness consequences (survival, growth, and reproduction), possibly altering the behaviour and ecology of a species in a given community (Goodale *et al.,* 2017). Because we detected such an influence in a continuous forest with low population density, stronger effects may be expected in smaller and more fragmented areas.

Conclusions

The two groups of howlers we studied were the same size, suggesting that the differences we observed in activity and ranging behaviour do not derive from group size. Our modelling revealed that the presence of conspecifics alters DPL but did not detect an influence of heterospecific presence on DPL, even though howlers frequently altered their behaviour after encountering other primate species. This suggests that intraspecific interactions influence ranging behaviours of howler monkeys more strongly than the presence of heteropecifics. Our two study groups exemplify two scenarios: one group (G4) lives in a large home range in the forest interior with primary forest (but an abundance of hillside habitats); their home range is not restrained in any direction; they have less contact with humans and more encounters with other species and more neighbouring groups. The other group (G3) resides in a secondary forest area at the edge of the forest, with frequent contact with humans and fewer encounters with other species and other groups but more frequent conspecific vocalizations. It is difficult to pinpoint which factor influences ranging behaviour the most. Small, fragmented, or highly anthropized environments can increase inter and intraspecific competition in howlers, and our study adds to the growing body of literature that shows how these interactions can disrupt their behaviour. Because moving is energetically costly, factors that lead to excessive movement may cause an energetic imbalance, compromising health and reproduction. Our study brings light to the intricate relationship that multiple species and multiple groups have on one another's behaviour.

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Inclusion and diversity statement

- One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science.
- One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community.
- While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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Authors and Affiliations

Gisela Sobral[1] · Lisieux F. Fuzessy[2] · Claudio Alvarenga de Oliveira[1]

✉ Gisela Sobral
gisasobral@gmail.com

[1] Departamento de Reprodução Animal, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, São Paulo, Brazil

[2] São Paulo State University, UNESP, Rio Claro, São Paulo, Brazil