

Ranging Patterns of Two Syntopic Howler Monkey Species (*Alouatta guariba* and *A. caraya*) in Northeastern Argentina

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Abstract To avoid competition, ecologically similar and closely related species tend to differ in their patterns of habitat use when they live in sympatry. We compared ranging patterns of brown howler (*Alouatta guariba*) and black and gold howler (*A. caraya*) monkeys living syntopically, i.e., co-occurring and overlapping their ranges in the same habitat within the zone of sympatry, in the Atlantic Forest of northeastern Argentina with the objective of evaluating whether their use of space contributes to the avoidance of interspecific competition for food resources. During 12 mo we collected data on the ranging behavior of 2 groups of each howler species. We analyzed annual and seasonal daily path lengths and movement rates, home range size, use and overlap, habitat and vertical strata use, and intergroup encounters. Black and gold howlers traveled farther and faster during the time of relative food abundance (abundant season) than during the time of relative food shortage (lean season), and their movement rates were affected by group identity and increased with the proportion of fruits in the diet. Brown howlers' traveling patterns were not affected by any of these factors. Home ranges for both species (95% fixed kernel; brown howlers: 31–70 ha, black-and-gold howlers: 17–112 ha) were among the largest recorded for *Alouatta*. For both species, core areas (50% fixed kernel) were larger for larger versus smaller groups, and decreased in the lean season

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compared to the abundant season. Both species showed similar patterns of habitat use, except for a slight vertical stratification. Groups of different species overlapped their ranging areas consistently more and responded to one another less aggressively during encounters than groups of the same species, suggesting that interspecific spatial niche separation for these two syntopic species is not occurring. The vertical stratification, as well as a day-to-day avoidance strategy, may be the only responses of species to one another that could reduce the potentially high levels of competition for food suggested by their elevated trophic niche overlap. A high degree of niche overlap may explain the parapatric distribution of howlers and other closely related and ecologically similar species of primates.

Keywords black-and-gold howlers · brown howlers · competition · daily path length · home range

Introduction

Researchers have studied ranging behavior to evaluate the importance of food competition that occurs within groups, between groups, and between species (Janson and Goldsmith 1995; Terborgh 1983; van Schaik 1989). Variability in ranging patterns observed in many primate species may result from differences in group size, seasonal changes in food availability, or the presence or absence of competitors. Across many primate species, observations of increasing home range size with increasing group size have been argued to be indicative of intragroup scramble competition. When food is limiting, larger groups should expand their home range to compensate for the increased food competition among individuals (Clutton-Brock and Harvey 1977; Milton and May 1976). Observations of longer daily path length with increasing group size may also be indicative of intragroup scramble competition in primates (Clutton-Brock and Harvey 1977; Dunbar 1988; Janson and Goldsmith 1995; cf. Sussman and Garber 2007). Primates may respond to a food shortage by either reducing daily ranges and feeding on lower quality food sources (= energy-minimizing strategy; e.g., *Alouatta palliata*, Milton 1980, 1998) or increasing daily ranges in search of high-quality food sources (= energy maximizing strategy; e.g., *Cebus apella*, Terborgh 1983). Finally, sympatric species may differ in ranging behavior, i.e., show spatial niche partitioning, especially during periods of low food availability, to minimize interspecific competition for resources (Waser 1987).

The majority of our knowledge on primate niche partitioning comes from studies on species showing large-scale sympatry, e.g., Ganzhorn (1989), Gautier-Hion *et al.* (1983), MacKinnon and MacKinnon (1980), and Terborgh (1983). In contrast, only a few researchers have investigated how closely related parapatric primate species respond to each other when occasionally co-occurring in contact zones, and they describe species pairs either greatly overlapping in their spatial niches, with a high potential to compete for limiting resources, e.g., *Lagothrix lagotricha* and *Ateles belzebuth* (Stevenson *et al.* 2000), or showing different habitat use and ranging patterns, as a result of interspecific differences evolved in allopatry, e.g., *Colobus guereza* and *C. angolensis* (Bocian 1997) and *Callicebus moloch* and *C. torquatus* (Kinzey and Gentry 1979). The study of 2 parapatric species in a contact zone

represents a unique opportunity to shed light onto the proximate mechanisms, e.g., interspecific competition or interspecific differences evolved in allopatry, responsible for maintaining parapatric distributions of closely related species.

Howlers (*Alouatta*) are folivorous-frugivorous Neotropical primates (Crockett and Eisenberg 1987). During times of food shortage, when they rely heavily on low-quality resources, e.g., mature leaves, howlers reduce their energy expenditure, behaving as energy minimizers (Milton 1980; Strier 1992). In addition, howlers' ranging patterns are significantly affected by the need to defend important resources (food and mates) from conspecific groups (Bravo and Sallenave 2003; Kowalewski 2007; Milton 1980; Sekulic 1982a, b), and by the presence of competing species (Waser 1987). Finally, howlers represent an excellent model for the study of the proximate mechanisms responsible for maintaining parapatric distributions of closely related species. In fact, howler species have an essentially parapatric distribution throughout the Neotropics, with a few narrow contact zones, where species pairs are sympatric and occasionally syntopic, i.e., co-occurring and overlapping their ranges in the same habitat within the zone of sympatry (Cortés-Ortiz *et al.* 2003; Groves 2001). For example, the only known contact zones between brown howlers (*Alouatta guariba* ssp. *clamitans*) and black and gold howlers (*Alouatta caraya*) lie in the Atlantic Forest of the Misiones province in northeast Argentina (Agostini *et al.* 2008) and in ecotonal areas between the Cerrado and the Atlantic Forest in south Brazil (Aguar *et al.* 2007; Bicca-Marques *et al.* 2008). Brown howlers are endemic to the Atlantic Forest of South America (Kinzey 1982). Black-and-gold howlers typically inhabit forests of Cerrado, Pantanal, and Chaco ecoregions (Rumiz 1990). Both species have similar body weights (brown howlers: average adult female = 4.55 kg, average adult male = 6.18 kg; black-and-gold howlers: average adult female = 4.33 kg, average adult male = 6.42 kg; reviewed by Di Fiore and Campbell 2007).

We here report the results of the first comparative study on the ranging behavior of 2 syntopic howler species. In particular, we compared the ranging behavior of brown howlers and black-and-gold howlers in the Atlantic Forest of Argentina. At this site, the 2 howler species show high trophic overlap throughout the year, indicating a great potential for food competition (Agostini *et al.* 2010). We examined and compared daily movements, home range and habitat use, vertical stratification, and patterns of intergroup encounters of these species living syntopically, during a 12-mo study, to assess whether patterns of range use contribute to ecological niche differentiation and avoidance of competition, and whether the ranging patterns of the 2 species are associated to the same proximate factors (i.e., climate, food availability, diet, group size, and relationships with neighboring groups).

If howlers are energy-minimizers, we predict that groups of both howler species will 1) reduce range areas, daily path lengths, and movement rates during periods of food scarcity compared to periods of food abundance; 2) reduce daily path lengths and movement rates according to the proportion of low-energy but evenly distributed foods, such as mature leaves, in their diet, and increase daily path lengths and movement rates according to the proportion of highly energetic and clumped resources, such as fruits, in their diet; 3) reduce daily ranging under extremely low as well as high temperatures, i.e., day range will show a negative curvilinear relationship with temperature, declining toward extremely low and high temperatures.

If howlers experience costs of intragroup food scramble competition, we predict that larger groups will have larger home ranges and will travel farther versus smaller groups. Finally, if food defense is most important in shaping intergroup relationships, we predict that 1) ranging overlap between howler groups (regardless of species) will be lower, and 2) intergroup encounters will be less frequent, more aggressive, and mostly in feeding contexts, during periods of food shortage, i.e., higher potential for food competition, versus periods of food abundance; and 3) overlapping groups will use different forest strata or different habitat types, especially in time of food scarcity. However, if mate defense is the most significant influence on intergroup relationships, we expect that 1) home ranges will overlap less between neighboring groups of the same species than between neighboring groups of different species, and 2) intergroup encounters between groups of the same species will be more aggressive than those between groups of different species, regardless of context. No horizontal (habitat) or vertical (strata) space partitioning between groups is expected under this hypothesis.

Methods

Study Site and Subjects

We conducted the study between December 2006 and November 2007 in El Piñalito Provincial Park ($26^{\circ}30'S$, $53^{\circ}50'W$), a 3,796-ha strictly protected area within the Atlantic Forest of Misiones, in northeast Argentina (Fig. 1). The climate is humid subtropical with a marked seasonality in temperature and day length, but not in rainfall (Crespo 1982). During the study year, monthly average temperature was

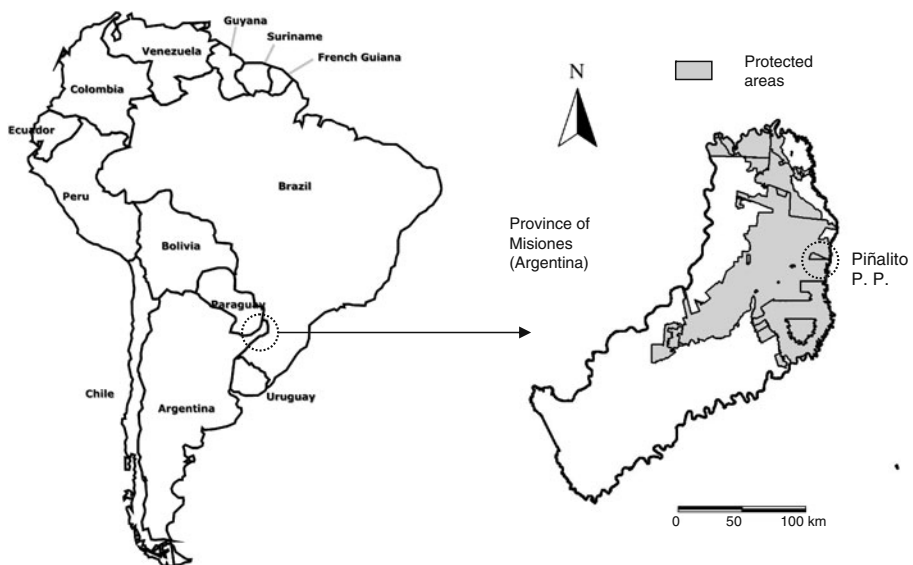


Fig. 1 Geographic location of the study area.

19.8°C (± 1.1 SE). A coldest season with shorter days occurred between May and August (average temperature: 15.1°C ± 0.8 SE; average day length: 10.6 h ± 0.2 SE), while the rest of the year was warmer (22.2°C ± 0.5 SE) with more hours of daylight (12.6 h ± 0.3 SE). Rainfall totaled 1,952 mm, with no marked seasonal pattern (Agostini 2009).

At the relative high altitude of El Piñalito (ca. 750 m asl), the typical vegetation is classified as a mixed forest with presence of the conifer *Araucaria angustifolia* (Brown and Zunino 1994). Intense timber exploitation occurred until late 1980s and, as a result, most of the park is covered by degraded primary forest. The area also includes 92 ha of old monospecific plantations of exotic pines *Pinus elliottii*, several trees of exotic *Eucalyptus* sp., and a small (6-ha) native *Araucaria* plantation.

We conducted the study on 2 groups of brown howlers, BR1 ($n=7-8$ individuals, excluding infants) and BR2 ($n=4$), and 2 groups of black-and-gold howlers, BL1 ($n=12-14$) and BL2 ($n=5-7$; Table 1). All 4 groups were previously habituated, and most group members were identified individually by natural markings.

Food Availability Estimates

To estimate the density, distribution, and abundance of plant resources available, we performed a vegetation survey of the 3 main habitat types (pine plantations, plantations of *Araucaria*, and native forest) within the home ranges of the study groups, in collaboration with 2 botanists (M. Srur and F. Gatti). We selected 209 points (20 m apart) along transect lines and identified and measured 4 trees ≥ 10 cm diameter at breast height (DBH) at each point, sampled using the point-quarter method (Krebs 1989). To estimate plant productivity, we established 2 phenological trails (total length = 6.65 km), partially crossing the focal groups' home ranges, in which we selected 253 trees with DBH ≥ 10 cm of 40 different species consumed by howlers [mean number of individuals per species \pm SE (range) = 6.2 \pm 2.6 (1–11)]. We monitored the trees on a monthly basis and estimated the abundance of each phenophase (expanding-young leaves, mature-senile leaves, flower buds, flowers, unripe fruits, and ripe fruits) in each tree as a fraction of the canopy volume, following an approximately logarithmic-scale index that ranged from 0 to 3 (Placci 1995). The phenological scores of individual trees of each species were averaged to

Table 1 Age-sex composition of the 4 focal groups (brown howlers: BR1, BR2; black- and-gold howlers: BL1, BL2) during the study period

Group	ADM	ADF	SBM	SBF	JVM	JVF	INF
BR1	1	3	1	0	2–3	0	0–2
BR2	1	3 ^a	0	0	0	0	2–3
BL1	1–2	5	1	0	0–2	4–5	1–3
BL2	1–2	1	1	0–1	1	0–2	0–1

^a One of the females was a black-and-gold howler adult female that migrated into the BR2 group before the beginning of the study period

ADM = adult male; ADF = adult female; SBM = subadult male; SBF = subadult female; JVM = juvenile male; JVJ = juvenile female; INF = infants

obtain a Phenological Index for the Species (PISp) for each monthly sample and for each phenophase. Then, we combined the phenological and vegetation survey data to calculate monthly indices of availability for each phenophase. For each food plant species, in each habitat type, we obtained a monthly Food Availability Index (FAI) by multiplying the PISp by the basal area (m^2/ha) estimated in the vegetation survey. Then, we calculated a FAI for each plant species as the average of the 3 habitat-specific FAIs, weighted by the proportion of representation of each habitat type in the entire study area. Finally, we calculated a monthly total FAI for each phenophase by adding FAI indices across all plant food species. Among fruits, we considered only fleshy ripe fruits because howlers fed mostly on this kind of fruit resources. We excluded *Ficus* sp., characterized by asynchronous fructification, owing to an evident mismatch in this resource availability between the trees we sampled and the trees actually available within groups' home ranges.

Ranging and Intergroup Encounters Data Collection

During the 12-mo study period, I. Agostini and I. Holzmann, with the help of 1 or 2 field assistants at a time, spent 3.02 d (± 0.6 SD; range 1–5) per month following each howler group. Overall, we collected 308 h of observation for group BR1, 352 h for BR2, 351 h for BL1, and 383 h for BL2. We collected data by scan sampling (Altmann 1974) at 10 min intervals. Except for a few gaps, when groups were out of view, scan sampling was continuous throughout the day, beginning as early as 0550 and finishing as late as 1930 h. During each scan (3 min in duration) we recorded the identity, activity and height from the ground of each individual in view. We refer to the observations of each scanned individual as a behavioral "record." Activities were divided into five mutually exclusive categories: resting, moving, feeding, socializing and other. The height of each scanned individual was estimated according to a 10-m scale: lower (0–10 m), middle (11–20 m), and upper (>20 m) strata. At the end of each scan, we obtained GPS readings of the location of the estimated center of group mass via a portable Garmin® GPS unit. We did not record readings unless the estimated position error displayed on the GPS unit was <20 m, obtaining readings for >90% of total scans for each study group. We recorded a total of 1,768 locations (33 d) for BR1, 1,939 locations (43 d) for BR2, 1,893 locations (35 d) for BL1 and 2,146 locations (34 d) for BL2.

We recorded an intergroup encounter whenever members of different groups were observed ≤ 50 m apart. We classified encounters as: "tolerant", when groups were indifferent to one another; "intermediate", when one or both groups showed slight avoidance movements and/or slight vocalizations in response to the presence of the other; or "aggressive," when individuals of at least one of the groups gave loud calls (howling) and/or chased members of the other group. We recorded the context of each group encounter, e.g., at feeding or sleeping sites.

Data Analysis

We analyzed ranging data via ArcView 3.2 and Animal Movement Analysis Extension (AMAE) to produce estimates of home range size, daily path length, and hourly movement rates (Hooge *et al.* 1999). We determined daily path lengths (DPL)

by summing the straight-line distances measured between consecutive GPS locations scored during daily group follows, and we averaged DPL values on a monthly basis. To estimate the mean hourly movement rates (MVR) for each month, we calculated the hourly rate of movement (DPL/h of observation) per day, and averaged per month. To estimate DPL and MVR, we included only complete days or days on which we followed a focal group for more than two-thirds of the day length (28 d for BR1, 30 d for BR2, 33 d for BL1, and 34 d for BL2).

For home range analysis, we used location records of both complete and incomplete days. We estimated home range size using the fixed kernel method, which represents the home range as the smallest area that incorporates a set percentage of the utilization distribution (Kernohan *et al.* 2001; Seaman and Powell 1996; Worton 1989). The 95% contour represents the home range, and the 50% contour represents the most intensively used areas or core areas (Hooge *et al.* 1999). For each group data set, we calculated an *ad hoc* reference smoothing factor (h_{ref}) following Worton (1989) and Blundell *et al.* (2001). Although our location data were not spatially independent, provided the time interval used is constant, autocorrelated locations may increase the accuracy and precision of kernel home range estimates, better reflecting patterns of use of space by individuals (Blundell *et al.* 2001; de Solla *et al.* 1999). We calculated home range and core area overlap between groups as the percent area each group shared with neighbors relative to the total home range or core area occupied by the group.

The 3 main habitat types in the study area were mapped using ArcView 3.2 and a Landsat 2004 satellite image of the park. For each group, we calculated the percentages of representation of each habitat type in the core area and in the entire home range. To determine the use of habitat in relation to activity, we calculated, for each habitat type, the proportions of GPS locations in which we scored 1 of 2 predominant activities (resting and feeding). We analyzed the vertical use of space by comparing monthly proportions of records of three main activities (resting, moving, feeding), for each stratum category.

Ranging variables were analyzed on an annual and seasonal basis. For analyses of seasonal variation in DPL, MVR, habitat and strata use, which were expressed as monthly means or proportions, we considered two seasons, classified on the basis of changes in food availability and temperature: a 4-mo lean season (May–August) that corresponded to the coldest season, and an 8-mo abundant season (September–April) that corresponded to the warmest season (Agostini *et al.* 2010). In contrast, for seasonal analyses of home range and core area size, use and overlap, we compared the lean season to 2 “partial” 4-mo abundant seasons, 1) November–February and 2) March, April, September, and November. We chose only 4 mo within the abundant season for sample size comparability between seasons, since home range size usually increases asymptotically with sampling effort (Di Bitetti 2001). We are aware of the possible bias of choosing only 2 particular 4-mo sets within the 8-mo abundant season. Ideally, one should use a resampling technique to compare the frequency distribution of all range sizes obtained by considering all the possible combinations of 4-mo sets of partial abundant season with the range size for the 4-mo lean season. However, calculating and comparing range size (and overlaps) for all possible 4-mo combinations is almost computationally impossible. Since we obtained very similar results in our two seasonal comparisons, and for simplicity, we present only data for

the November–February 4-mo set here, assuming it was representative for the entire abundant season.

The study period was divided into 12 monthly samples for the 4 groups, except BR1, which lacks the October sample. We obtained each sample ≤ 10 d of the 2-d periods of plant phenology monitoring, so that behavioral observations can be tightly correlated with monthly estimates of food availability.

We used parametric tests whenever residuals of data were normally distributed (once the statistical model had been fitted); otherwise, we used nonparametric statistics (Sokal and Rohlf 1995). We performed 1-way ANOVAs to compare DPL and MVR across groups, and to test the effect of season on DPL and MVR, within each howler species. Then, we generated a stepwise multivariate ANCOVA model to determine the effect of variables such as group identity; season; availability and proportions of young leaves, mature leaves, fruits, and flowers in the diet; rainfall; and average maximum and minimum temperatures on MVR within each howler species. To analyze the relationship between MVR and temperature, which was predicted to be curvilinear by one of our hypotheses, we performed both a linear and a curvilinear (2-degree polynomial) regression of residuals of the final ANCOVA model on minimum and maximum temperatures. We used a linear regression to assess the relationship between group size and home range or core area size, and an ANCOVA to test the effects of the covariate group size and the independent variable, species, on home range size and on the relative size of core area relative to home range. We used a Mann-Whitney *U*-test to evaluate the effect of activity on the use of each habitat type, and a 3-way ANOVA to test the effect of group identity, season, and activity on the use of each forest stratum. Finally, we performed G-tests to compare the observed versus expected frequencies of group encounters in the abundant and lean season (we calculated expected frequencies on the basis of the total number of hours of observation in each season), and to test the independence of intra- or interspecific encounters and reactions (we lumped intermediate and aggressive reactions to increase the expected frequencies). All statistical tests were 2-tailed with α set at 0.05, and performed via Statistica 5.5 (Statsoft, Inc.) and JMP 3.2.2 (SAS Institute).

Results

Daily Path Length and Movement Rates

On average (\pm SE), howler groups traveled between 709 ± 59 m and 840 ± 95 m each day (Table II), and monthly mean DPL did not significantly differ among the 4 groups (1-way ANOVA: $F_{3,43}=0.47$, $p=0.706$). Black-and-gold howler groups traveled significantly farther in the abundant season than in the lean season ($F_{1,22}=15.07$, $p<0.001$), while brown howler groups did not vary their daily journey according to seasons ($F_{1,21}=0.48$, $p=0.494$). Similarly, mean MVR ranged from 70 to 93 m/h among groups (Table II), and it did not significantly differ among the 4 howler groups ($F_{3,43}=1.12$, $p=0.351$). However, whereas black-and-gold howler groups traveled faster in the abundant season than in the lean season ($F_{1,22}=5.54$, $p=0.028$), brown howler groups did not show any difference in MVR between seasons ($F_{1,21}=0.18$, $p=0.680$). For black-and-gold howlers, MVR significantly increased with

Table II Yearly and seasonal monthly mean (\pm SE) and range values of daily path length (DPL) and monthly mean (\pm SD) movement rates (MVR) for the 2 brown howler groups (BR1 and BR2) and the 2 black-and-gold howler groups (BL1 and BL2)

Group	No. of months (no. of days)	Monthly mean \pm SE DPL (m)	Range DPL	Monthly mean \pm SD MVR (m/h)
Yearly				
BR1	11 (28)	759 \pm 71	244–1,666	81 \pm 24
BR2	12 (30)	744 \pm 95	75–1,538	83 \pm 39
BL1	12 (33)	840 \pm 95	62–1,582	93 \pm 37
BL2	12 (34)	709 \pm 59	228–1,308	70 \pm 20
Abundant season				
BR1	8 (18)	787 \pm 108	260–1,666	75 \pm 24
BR2	8 (19)	777 \pm 119	228–1,436	84 \pm 41
BL1	8 (22)	973 \pm 95	397–1,582	104 \pm 33
BL2	8 (24)	819 \pm 33	496–1,308	78 \pm 12
Lean season				
BR1	4 (10)	709 \pm 58	244–1,183	91 \pm 24
BR2	4 (11)	680 \pm 180	75–1,538	81 \pm 42
BL1	4 (11)	574 \pm 147	62–1,126	72 \pm 38
BL2	4 (10)	488 \pm 94	228–1,092	53 \pm 21

Abundant season: December 2006–April 2007 and September–November 2007; lean season: May–August 2007

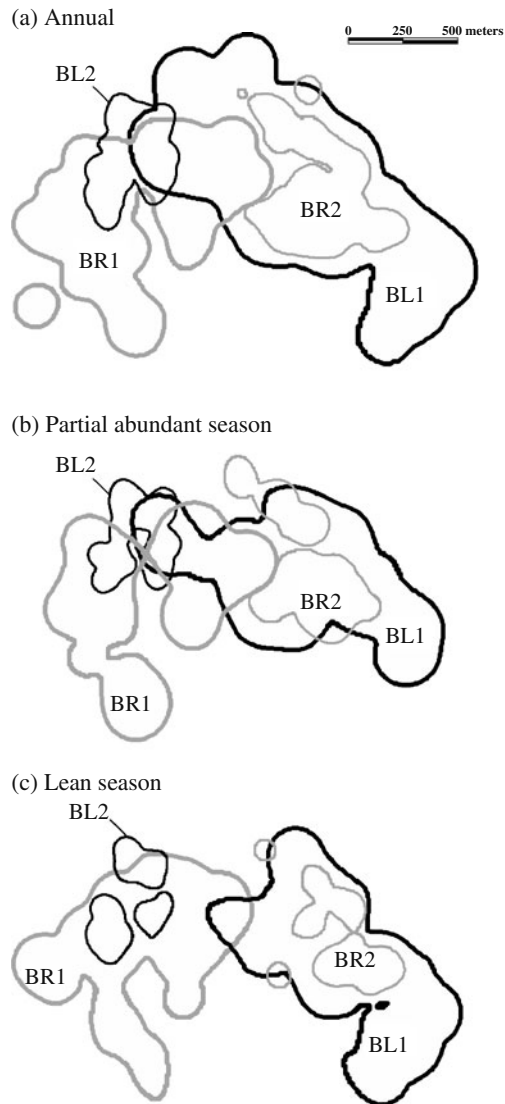
the proportion of fruits in diet and was greater for BL1 than BL2 (effect of % fruit in diet: $F_{1,1}=11.17$, $p=0.003$; effect of group identity: $F_{1,1}=9.17$, $p=0.006$; $R^2_{adj}=0.39$). All other variables showed no statistically significant effect on MVR. Finally, for brown howlers we did not find a significant effect of any variable on the MVR.

Home Range Size and Use

Within each howler species, larger groups had consistently larger annual home range areas than smaller groups (Fig. 2a; Table III). Ninety-eight percent of the variation in home range size was explained by group size and species (besides the effect of group size, home ranges of brown howlers may be larger than those of black-and-gold howlers; ANCOVA; effect of group size: $F_{1,1}=171.73$, $p=0.049$; effect of species: $F_{1,1}=25.71$, $p=0.124$, $R^2_{adj}=0.98$). For all groups, except BR1, the size of ranging areas decreased slightly from the abundant to the lean season (Fig. 2b,c; Table III).

Within each howler species, larger groups had consistently larger annual core areas than smaller groups (Table III). There was a positive and statistically significant linear relationship between the annual core area size and mean group size [$F_{1,2}=36.87$, $P=0.026$, $R^2_{adj}=0.92$]. The relative size of core areas with respect to the annual home range was consistently greater for larger groups compared to smaller groups within each species, and greater for black and gold howler (24.2% for BL1 and 13.6% for BL2) compared to brown howler groups (10.5% for BR1 and 6.6% for BR2). Ninety-nine percent of the variation in the relative size of core areas

Fig. 2 Home ranges for brown howler BR1 (gray thicker line contour) and BR2 (gray thinner line contour) groups, and black-and-gold howler BL1 (black thicker line contour) and BL2 (black thinner line contour) groups (a) over the entire study year, (b) in the partial abundant season (November–February), and (c) in the lean season (May–August), in El Piñalito Provincial Park. Home ranges are estimated as 95% fixed kernels.



in relation to annual home range was explained by group size and species, although this result was not statistically significant, probably due to the small sample size (ANCOVA; effect of group size: $F_{1,1}=81.35$, $p=0.070$; effect of species: $F_{1,1}=24.62$, $p=0.127$, $R^2_{adj}=0.99$). Finally, for all 4 groups, core area size decreased consistently from abundant to lean season (Table III).

Range Overlap Between Groups

Over the study year, 2 pairs of groups of the 2 species overlapped extensively in their home ranges and core areas, while groups of the same species showed little (black-and-gold howler) or no overlap (brown howler; Fig. 2a; Table IV).

Table III Yearly and seasonal home range size (ha) estimated by 95% fixed kernel analysis, and core area sizes estimated as 50% fixed kernel analysis for the 2 brown howler groups (BR1 and BR2) and the 2 black-and-gold howler groups (BL1 and BL2)

Group	95% Kernel	50% Kernel
Yearly		
BR1	70.32	7.39
BR2	31.22	2.05
BL1	111.91	27.03
BL2	17.32	2.36
Partial abundant season		
BR1	59.44	7.57
BR2	26.17	3.01
BL1	71.42	9.45
BL2	14.33	1.48
Lean season		
BR1	60.37	5.79
BR2	16.32	1.33
BL1	67.74	4.79
BL2	11.82	0.97

We calculated *ad hoc* reference smoothing factors following Worton (1989) and Blundell *et al.* (2001). Partial abundant season: December 2006–February 2007 and November 2007; lean season: May–August 2007

Encounters observed between our focal groups and other neighboring nonfocal groups also indicate a small degree of intraspecific overlap for both species. Ranging areas or core areas also overlapped between groups of the 2 species to a greater extent than between groups of the same species when we considered the abundant and the lean season separately (Fig. 2b,c; Table IV). While in the lean season, all groups, especially the smallest ones (BR2 and BL2), shared significant portions of their ranging area and core areas with groups of the other species, in the abundant

Table IV Yearly and seasonal home range and core area percentage overlap of each group (brown howler [BR1 and BR2] and black-and-gold howler [BL1 and BL2]) with groups of the other species (INTERSP) or with the group of the same species (INTRASP)

Group	Home range overlap (%)		Core area overlap (%)	
	INTERSP	INTRASP	INTERSP	INTRASP
Yearly				
BR1	40.58	0	54.43	0
BR2	98.75	0	50.02	0
BL1	46.19	5.87	15.36	0.28
BL2	75.36	37.92	41.21	3.22
Partial abundant season				
BR1	34.37	0	0	0
BR2	83.22	0	0	0
BL1	52.74	8	0	0
BL2	51.49	40	0	0
Lean season				
BR1	21.88	0	16.67	0
BR2	93.25	0	71.25	0
BL1	27.28	0	19.83	0
BL2	84.10	0	100	0

Partial abundant season: December 2006–February 2007 and November 2007; lean season: May–August 2007

season, groups of the 2 species shared parts of their ranging areas but used nonoverlapping core areas. Groups of the same species did not overlap in their core area at all, regardless of season (Table IV).

Habitat Use

The 165-ha area occupied by the focal groups was 32% pine plantations (PP), 4% *Araucaria* plantations (AP), and 64% native forest (NF). Howlers tended to use PP more for resting and NF more for feeding (Mann-Whitney for PP: $U_{47,47}=851.5$, $p=0.056$). A greater proportion of the core areas of all focal groups were represented by monospecific plantations (PP=46–63%; AP=0–12%) than by native forest (NF=37–49%, Fig. 3). All groups increased the proportion of PP and all groups, except for BL1, decreased the proportion of NF in their core areas from the abundant to the lean season. Group BL1 included AP in their core areas only in the abundant season (Fig. 3). All groups, except BR2, used PP consistently more and NF consistently less than expected on the basis of the representation of these habitats in their home ranges, and this trend was more pronounced in the lean season. Habitat use of BR2 group was close to what it would be expected on the basis of habitat representation in its home range. However, BR2 was the only group that contained more PP than NF in its home range in absolute terms (Fig. 3).

Use of Forest Strata

All 4 groups used mainly upper and middle levels of the vegetation (Fig. 4). Black-and-gold howler groups used the middle stratum more and the upper stratum less than brown howler groups, and whereas subjects used the middle stratum mainly for feeding and moving, they used the upper stratum mainly for resting. The effect of season on monthly percentages of use of strata was not statistically significant (3-way ANOVA, Middle stratum as dependent variable; group effect: $F_{3, 116}=13.45$,

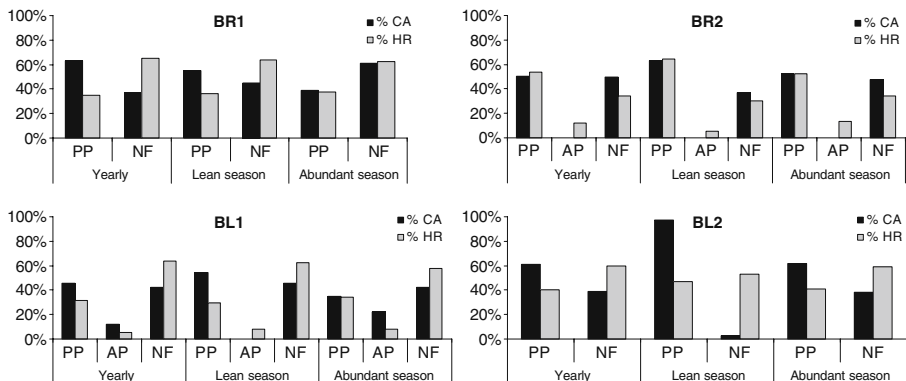


Fig. 3 Yearly and seasonal percentage areas represented by each habitat type in the core area (black bars) and in the home range (gray bars) for brown howler (BR1 and BR2) and black-and-gold howler (BL1 and BL2) groups. CA = core area, HR = home range, AP = *Araucaria* plantations, PP = Pine plantations, NF = native forest.

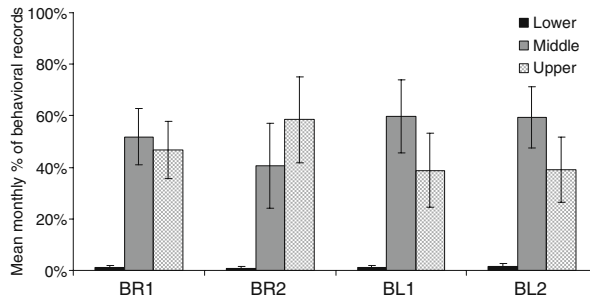


Fig. 4 Mean (\pm SD) monthly percentage use, i.e., mean monthly percentage of behavioral records of different forest strata (Lower, Middle, Upper) by the brown howler (BR1 and BR2) and black-and-gold howler (BL1 and BL2) groups during the study year.

$p < 0.001$, Fig. 4; activity effect: $F_{2, 116} = 7.2$, $p = 0.001$; season effect: $F_{1, 116} = 1.79$, $p = 0.184$; because all groups only occasionally used the Lower stratum, proportional use of Middle and Upper strata are dependent on each other).

Intergroup Encounters

We observed 29 intergroup encounters, of which 11 involved confrontations with nonfocal groups ($n=6$) or solitary individuals ($n=5$) present in the area. Only 6 encounters, mostly interspecific, involved feeding contexts (Table V). Overall, howler groups displayed significantly more aggressive reactions in encounters with groups of the same species and more pacific reactions in encounters with groups of

Table V Number of interspecific (INTERSP) and intraspecific (INTRASP) intergroup encounters according to their nature (TOL = tolerant, INT = intermediate, AGG = aggressive) in different contexts (Feeding, Sleeping sites, and Other, which includes resting, traveling or unknown activities), on a yearly and seasonal basis

	Context	INTERSP			INTRASP		
		TOL	INT	AGG	TOL	INT	AGG
Yearly	Feeding	3	1	1	0	0	1
	Sleeping	2	0	0	0	0	6
	Other	8	1	0	1	0	5
	Total	13	2	1	1	0	12
Abundant season (8 mo)	Feeding	2	1	1	0	0	1
	Sleeping	2	0	0	0	0	4
	Other	5	1	0	1	0	1
	Total	9	2	1	1	0	6
Lean season (4 mo)	Feeding	1	0	0	0	0	0
	Sleeping	0	0	0	0	0	2
	Other	3	0	0	0	0	4
	Total	4	0	0	0	0	6

different species ($G=17.68$, d.f.=1, $p<0.001$; Table V). Finally, frequencies of both inter- and intraspecific group encounters did not significantly differ between seasons (G -test, interspecific encounters: $G=0.01$, d.f.=1, $p=0.916$; intraspecific encounters: $G=1.23$, d.f.=1, $p=0.267$).

Discussion

Our study has 3 limitations that are important to acknowledge before exploring the implications of our results: a small number of groups investigated, a relatively restricted spatio-temporal study frame (1 specific locality and 1 annual cycle), and the particular anthropogenic habitat mosaic (plantations and forest) characterizing the study area. Nevertheless, our study, which is the first investigating ranging behavior of 2 syntopic howler species, represents a fundamental contribution to a better understanding of the ecological relationships between 2 parapatric species in a contact zone, a relatively understudied issue in primate ecology.

Home Range Size and Daily Ranging

The home ranges of brown howlers and black-and-gold howlers at El Piñalito are among the largest recorded for *Alouatta* (Crockett and Eisenberg 1987; Di Fiore and Campbell 2007). The size of howlers' home ranges may depend on group size, habitat quality, as well as population density and presence of competitors (Crockett and Eisenberg 1987). At our site, all focal groups' home ranges included large portions of monospecific conifer plantations, which are lower-quality habitats compared to native forest (Agostini 2009). Moreover, both howler populations live at extremely low densities (0.10 ind/ha and 0.15 ind/ha for brown howlers and black-and-gold howlers, respectively; Agostini, *unpubl. data*) compared to other sites (Crockett and Eisenberg 1987; Di Fiore and Campbell 2007). Finally, owing to their high interspecific trophic overlap, syntopic brown and black-and-gold howlers represent potential competitors to each other in the area (Agostini *et al.* 2010). All 3 factors probably interact to produce the extremely large home ranges observed for howlers at El Piñalito. In contrast, daily path lengths recorded for both species at El Piñalito were well within the range of variation seen for howlers across sites (Crockett and Eisenberg 1987; Di Fiore and Campbell 2007), supporting the view that day range may be physiologically constrained for howlers owing to their high level of consumption of low-energy food, such as mature leaves (Janson and Goldsmith 1995; Milton 1980).

Influence of Group Size on Ranging

At our study site, within each species, larger groups had larger home ranges versus the smaller ones. This finding supports the hypothesis that groups of both species may have experienced some levels of intragroup food scramble competition (Clutton-Brock and Harvey 1977; Isbell 1991). Interestingly, the influence of group size on ranging area was more clearly evident in the core area size than in the home range size, likely because the core area represents the minimum area that each

howler group needs to survive. However, we did not find any clear relationship between group size and daily path length for our focal species. Researchers have reported the lack of a significant relationship between group size and day range across many folivorous primate species (Clutton-Brock and Harvey 1977; Fashing 2001; Yeager and Kirkpatrick 1998), and explained it either as an evidence of little or no intragroup scramble competition experienced by folivores (Isbell 1991), or as a result of their inability to increase their daily energy output (and thus daily ranging distance) because of the low energy return rate per unit digestion time (Janson and Goldsmith 1995). The latter hypothesis could explain why many folivorous primates usually minimize their daily energy expenditure when food is in short supply (Milton 1980, 1998; Oates 1977; Strier 1992).

Influence of Food Seasonality, Diet, and Climate on Ranging

Black-and-gold howler groups at El Piñalito reduced their mean daily path length and movement rate during the season of low food availability as predicted under the energy-minimizing strategy hypothesis (Milton 1980). During the lean season, both howlers increase the consumption of low-quality but evenly distributed foods, such as mature leaves (Agostini *et al.* 2010). By reducing the daily travel speed and distance, howlers may be able to minimize the energetic expenditure in this critical period (Milton 1980; Strier 1992). In contrast, brown howler groups did not change their daily journeys and movement rates with food seasonality.

For black-and-gold howlers, increasing proportions of fruits in diet determined an increase in the rates of movement, suggesting that, when ingesting high-energy foods such as fruits, black-and-gold howlers may gain sufficient energy to travel farther and faster between fruit patches. This is fully consistent with predictions of the energy-minimizing hypothesis. We did not find the predicted curvilinear relationship between movement rates and temperatures, probably owing to the lack of extremely high temperatures during group follows during our study. However, an exceptionally low rate of movement (16.7 m/h) for BL1 group in July (the coldest month) constitutes (somewhat anecdotal) evidence that when minimum temperatures are very low, black- and-gold howlers save energy. Again, ranging patterns of brown howlers were not significantly affected by any factor. The differences found in the way black-and-gold howlers' and brown howlers' daily ranging responds to behavioral (diet) and environmental factors (seasonality) at our site may be explained either by different species-specific physiological constraints, or by different distribution of particular fruit trees consumed. An experiment, in which fruit patches abundance and distribution are artificially regulated, e.g., feeding platforms (Janson 1998), could help to tease apart the possible factors determining this interspecific difference.

Home Range, Habitat, and Strata Use

Both howler species showed a more concentrated pattern of use of space, i.e., smaller core areas during the lean season compared to the abundant season, while they maintained similar overall ranging areas in the 2 seasons. Likely, the maintenance of relatively constant range areas is associated to the need to patrol

and defend territorial boundaries against neighboring groups. Both howlers rested more frequently in pine plantations, but fed more frequently in the native forest, where they could find most of the food tree species (Agostini 2009). The increasing use of pine plantations by all howler groups in the lean season could be explained by their reliance on male cones of *Pinus elliottii* or mature leaves of vines which were abundant in the pine plantations at this time, when food items from native trees were scarce (Agostini *et al.* 2010).

Although both species used upper strata preferentially for resting and middle strata preferentially for feeding and moving, brown howlers showed a preference for upper strata, whereas black-and-gold howlers showed a preference for middle strata. This slight stratification, which is seen also for feeding heights at our site, could be the result of specific adaptations to gradients of leaf quality across strata (Agostini 2009).

Intergroup Spacing Patterns

The patterns of intergroup encounters and ranging overlap we found do not support the hypothesis that food competition is the main factor shaping intergroup relationships both intra- and interspecifically. In fact, only a few intra- and interspecific group encounters, in both seasons, involved feeding contexts (Table V), and only conspecific black-and-gold howler groups showed a consistent pattern of lower ranging overlap during the lean season than during the abundant season. Groups of different species overlapped extensively without any clear seasonal variation. Moreover, whereas core areas of conspecific groups never overlapped, core areas of groups of the 2 species overlapped extensively only during the lean season and diverged completely during the abundant season, in contrast with predictions of the hypothesis that intergroup relationships were shaped by food competition. However, during the lean season, food resources are so scarce that groups of both species may be constrained to intensively use the same small areas that contained the few available high-quality foods. The intensity of food competition at this critical time of the year could be reduced by the vertical stratification of groups of the 2 species, as well as by a day-to-day avoidance strategy, e.g., intergroup spacing regulation via long-distance calls (da Cunha and Byrne 2006). Avoidance between groups is suggested by the fact that, although groups of different species overlapped in their core areas consistently more in the lean season than in the abundant season, interspecific encounter rates did not significantly differ between seasons.

Overall, the patterns of intergroup ranging overlap and encounters at our study site support the hypothesis that intergroup relationships are shaped by mate defense. In fact, the lower overlap and the more aggressive nature of encounters within species than between species could be explained on the basis of sexual competition, which should be high within species and nearly absent between species. However, we cannot exclude that, given the rareness of syntopy between brown howlers and black-and-gold howlers throughout their distributions (Cortés-Ortiz *et al.* 2003), groups of the 2 species, though currently competing for food, did not evolve the same territorial responses, e.g., loud calls and chasings, to one another as those showed within each species. Even though our observed pattern of home range

clearly suggests a higher overlap between groups of different species than between groups of same species, it is important to note that for each group we studied there were 2 groups of the other species and only 1 conspecific group with which they could have overlapped. Thus, one would expect, just by chance, that it will overlap more extensively with a group of the other species.

In conclusion, at El Piñalito, groups of brown and black-and-gold howlers, which overlap greatly in their diet throughout the year (Agostini *et al.* 2010), also showed extensive overlap in their ranging, suggesting that no spatial niche separation occurs for these 2 syntopic species. The slight vertical stratification, as well as a day-to-day avoidance strategy, may be the only interspecific responses that reduce potentially high levels of competition at our study site. The high degree of niche overlap and the potential for interspecific competition could be responsible for maintaining sharp biogeographic boundaries, i.e., parapatric distributions, among ecologically similar and closely related primate species such as *Alouatta* spp. Together with habitat loss and fragmentation and susceptibility to diseases, interspecific competition with black-and-gold howlers could be preventing the recovery of the small endangered population of brown howlers in northeast Argentina (Díaz and Ojeda 2000).

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