

RESEARCH ARTICLE

Are Howler Monkey Species Ecologically Equivalent? Trophic Niche Overlap in Syntopic *Alouatta guariba clamitans* and *Alouatta caraya*ILARIA AGOSTINI^{1,2*}, INGRID HOLZMANN^{2,3}, AND MARIO S. DI BITETTI^{2,3}¹Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy²Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú, Misiones, Argentina³Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Instituto de Biología Subtropical, Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Puerto Iguazú, Misiones, Argentina

According to the principle of competitive exclusion, niche differentiation allows the stable coexistence of closely related species. We analyzed dietary profile and diversity, and dietary overlap between syntopic brown howlers (BR; *Alouatta guariba clamitans*) and black and gold howlers (BLG; *A. caraya*) in the Atlantic Forest of NE Argentina, with the objective of evaluating the degree of trophic niche overlap and potential interspecific competition for food. During 12 months, we collected data on feeding behavior of two groups of each howler species using the scan sampling method, together with data on food availability. Both at the group- and species-level, we analyzed feeding behavior in terms of monthly percentages of time spent feeding on each food type and specific food item, dietary diversity (Shannon index H'), and we estimated dietary overlap using the percentage index and the Morisita–Horn index (C_H). Across months, both howlers showed species-specific preferences for certain food items, and BLG had a more diverse diet (mean \pm SE, $H' = 2.77 \pm 0.08$) than BR ($H' = 2.39 \pm 0.09$). However, diets of both species overlapped extensively (percentage index = $45.64 \pm 2.97\%$; $C_H = 0.6 \pm 0.05$) and diets of conspecific groups did not overlap more than diets of groups of different species. Given their high degree of trophic overlap, syntopic BR and BLG meet one of the conditions necessary for interspecific food competition to occur. Although at present we lack direct evidence for interspecific competition in these howler species, we conclude that high levels of niche overlap may have an important role in maintaining the essentially parapatric distribution of howler species throughout the Neotropics. *Am. J. Primatol.* 72:173–186, 2010. © 2009 Wiley-Liss, Inc.

Key words: Argentina; black and gold howlers; brown howlers; contact zone; interspecific competition

INTRODUCTION

The principle of competitive exclusion predicts that, in a stable environment, similar species can coexist successfully through niche differentiation [Begon et al., 1990; Schoener, 1974]. The extent to which similarity in resource use relates to competition between species has been highly debated among ecologists [Begon et al., 1990; Tokeshi, 1999]. However, when taking into account the distributions of two ecologically similar species, it is clear that some patterns, such as parapatry or complementary occurrences, may be maintained by interspecific competition, as well as by environmental gradients, differential pressures of predators, parasites or diseases, reproductive interference, or density-dependent dispersal [Bull, 1991]. Two species arising from geographical separation after splitting of an ancestral lineage may overlap if they secondarily come to live in sympatry. In this case, when resources are in limited supply, a high overlap in resource use is one possible indication of interspecific competition [Tokeshi, 1999].

Resource partitioning has been documented frequently in primates [e.g., Ganzhorn, 1988, 1989; Gautier-Hion, 1980; Struhsaker & Oates, 1975; Terborgh, 1983]. Primates represent good subjects for such studies, because they generally live in communities in which other primate species are a significant component and where interspecific

Contract grant sponsor: Argentinean Consejo Nacional de Investigaciones Científicas y Técnicas; Contract grant number: PIP 6318; Contract grant sponsors: Cleveland Metropark Zoo (Scott Neotropical Fund); Primate Conservation Inc.; Conservation International (Primate Action Fund); International Primatological Society (Conservation Grant); Idea Wild.

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Received 19 May 2009; revised 26 October 2009; revision accepted 29 October 2009

DOI 10.1002/ajp.20775

Published online 1 December 2009 in Wiley InterScience (www.interscience.wiley.com).

interactions, such as competition or mutualism, are frequent [Waser, 1987]. However, except for several studies of mixed-species troops of tamarins and mixed-species troops of tamarins and callimicos [e.g., Garber & Leigh, 2001; Heymann & Buchanan-Smith, 2000], most of the comparative studies on primate assemblages have been carried out on Old World primates. This bias is not due to the degree of primate community species richness [Fleagle & Reed, 1999], because many Neotropical forests reach primate diversity values comparable to those of the richest African and Asian sites [Terborgh, 1983].

Most comparative studies on niche differentiation in primates have been carried out on species occurring in sympatry, and have generally demonstrated high interspecific dietary overlap, with some degree of separation in forest stratum use [e.g., cercopithecines: Buzzard, 2006; Cords, 1986; callitrichins: Garber, 1988, 1993; Gautier-Hion, 1980; Heymann & Buchanan-Smith, 2000; lemurs: Overdorff, 1993; Simmen et al., 2003; Vasey, 2000]. In these studies, as well as in studies on other sympatric mammals [Dunbar, 1978; Emmons, 1980] and birds [Smith et al., 1978], the importance of interspecific competition has been assessed by comparing the dietary overlap during periods of low vs. high food availability, following the ecological theory according to which, in fluctuating environments, two potential competitors must diverge to a greater degree in resource use in times of resource scarcity than during times of resource abundance, if they are to coexist [Pyke et al., 1977; Schoener, 1982]. Moreover, on the basis of the classic Lotka-Volterra models, according to which interspecific competition must be weaker than intraspecific competition for at least one of two sympatric species if they are to coexist [Tokeshi, 1999], it has been suggested that a further indicator of the importance of interspecific competition can be obtained by comparing inter- and intraspecific dietary overlap [Buzzard, 2006; Cords, 1986; Gautier-Hion, 1980; Vasey, 2000, 2002; Waser, 1987]. In fact, whenever niche overlap between species pairs remains as great as that within species and resources are limited, the potential for interspecific competition is expected to be high [Waser, 1987].

Although the majority of our knowledge concerns species showing large-scale sympatry, very little is known about how primate species with parapatric distributions respond to each other when they occasionally co-occur in narrow contact zones [Bocian, 1997; Dew, 2005; Kinzey & Gentry, 1979; Stevenson et al., 2000]. Howlers (genus *Alouatta*, Atelidae) are large-bodied, arboreal, folivorous-frugivorous primates that have the largest distribution and occupy the widest range of habitat types of any Neotropical primate [Crockett & Eisenberg, 1987]. The ten howler species currently recognized are found in an essentially parapatric distribution [Cortés-Ortiz et al., 2003; Groves, 2001]. Owing to overall similarity in the set of ecological

requirements and behavioral adaptations that characterizes all howler species throughout their distributions [e.g., interspecific differences in howler diets, ranging, and activity patterns are smaller than habitat and seasonal intraspecific differences; Crockett & Eisenberg, 1987], they have been classified as ecospecies, i.e., a group of ecologically equivalent (and mutually exclusive) congeners usually representing parapatric replacements across sharp biogeographical boundaries [Peres & Janson, 1999]. Although relatively rare, a few narrow contact zones, where species pairs are occasionally syntopic, have been reported [Agostini et al., 2008; Aguiar et al., 2007, 2008; Bicca-Marques et al., 2008; Büntge & Pyritz, 2007; Chames & Olmos, 1997; Cortés-Ortiz et al., 2007; Defler, 2004; Di Bitetti et al., 1994; Iwanaga & Ferrari, 2002; Pinto & Setz, 2000; Wallace et al., 1998]. In particular, in NE Argentina and S Brazil, there is evidence of one of the few known contact zones between brown howlers (BR; *Alouatta guariba* ssp. *clamitans*) and black and gold howlers (BLG; *A. caraya*) [Agostini et al., 2008; Aguiar et al., 2007; Bicca-Marques et al., 2008; Di Bitetti et al., 1994], two morphologically and genetically well-differentiated species [Cortés-Ortiz et al., 2003; Gregorin, 2006; Groves, 2001]. *A. guariba* and *A. caraya* belong to two different sister clades that appear to have come secondarily into contact in the region [Cortés-Ortiz et al., 2003]. BR are endemic to the Atlantic Forest [Kinzey, 1982] and are frequently associated with mature forests [Di Bitetti et al., 1994]. BLG usually inhabit secondary riverine and inland forests throughout the Cerrado, Chaco, and Pantanal ecoregions [Rumiz, 1990], occasionally spanning some ecotonal zones at the edge of the Atlantic Forest in Southern Brazil [Aguiar et al., 2007; Gregorin, 2006]. A small and unstudied population of BLG lives in the Atlantic Forest of Northeastern Argentina at relatively low densities [Zunino et al., 2001]. Because variation in the patterns of habitat and resource utilization by non-syntopic brown howler and black and gold howler populations in Southern Brazil is more easily explained by site-specific differences in food availability and habitat characteristics than by interspecific differences, habitat and resource utilization are not expected to represent the mechanisms of segregation for BR and BLG when they live in syntopy [Bicca-Marques et al., 2008]. Given their similar ecology and the narrow area of coexistence, syntopic BR and BLG may potentially compete for resources. To evaluate the potential for interspecific competition, we carried out the first comparative study on the feeding ecology of these two howler species living in syntopy in El Piñalito Provincial Park, located in the Atlantic Forest of Misiones, Northeastern Argentina, using direct observational data from a 12-month study on two groups of each species, and measurements of food availability for

the study area. We hypothesized three different scenarios: (1) if syntopic BR and BLG show differences in diet as a result of adaptations that evolved in allopatry to different habitats, we expect their dietary overlap to be relatively low throughout the year and to vary little according to food availability. Under this scenario we predict that intraspecific overlap in diet and feeding ecology would be consistently higher than interspecific overlap throughout the year. (2) Alternatively, if syntopic BR and BLG show differences in diet due to a plastic response of each species to the presence of a congeneric potential competitor, we expect the two howler species to reduce their dietary overlap during periods of food shortage, otherwise showing essentially the same diet. (3) Finally, if the two syntopic howler species are ecologically equivalent, we expect them to overlap extensively in their diet throughout the year, with no significant difference in overlap in response to changes in food availability, and no difference between intra- and interspecific overlap across the year.

METHODS

Study Site and Species

This study took place 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 Northeastern Argentina (Fig. 1). The climate is humid and subtropical with a marked seasonality in temperature and day length, but not in rainfall

[Crespo, 1982]. During the study period (December 2006–November 2007), rainfall totaled 1,952 mm with no marked seasonal pattern, and monthly average maximum and minimum temperatures were $24.3^{\circ}C (\pm 1.1 SE)$ and $15.4^{\circ}C (\pm 1.1 SE)$, respectively. There was a cold season between May and August when frosts were common. Climatic data were provided by the Argentinean National Meteorological Service at Irigoyen, located approximately 40 km from our study site.

At the relative high altitude of El Piñalito (ca. 750 m asl), the typical vegetation is classified as a mixed forest dominated by the Paraná pine, *Araucaria angustifolia* (Araucariaceae) [Brown & Zunino, 1994]. However, due to the intense timber exploitation that occurred until the late 1980s, most of the park is covered by a highly degraded forest and a small portion of secondary forest, which includes 92 ha of old (>30 yr) monospecific plantations of exotic pines *Pinus elliottii* (Pinaceae), with a few trees of exotic *Eucalyptus* sp. (Myrtaceae), and native Paraná pines.

We carried out a behavioral study on two groups of BR, BR1 ($N = 7-8$ individuals, excluding infants) and BR2 ($N = 4$), and two groups of BLG, BLG1 ($N = 12-14$) and BLG2 ($N = 5-7$) (Table I). The BR2 group included an adult female BLG as resident member. Regardless of the species, larger groups had larger home ranges (BR1: 70 ha; BLG1: 112 ha) than did smaller groups (BR2: 31 ha; BLG2: 17 ha), whereas day ranges were similar across all groups [Agostini et al., in press]. In addition, although

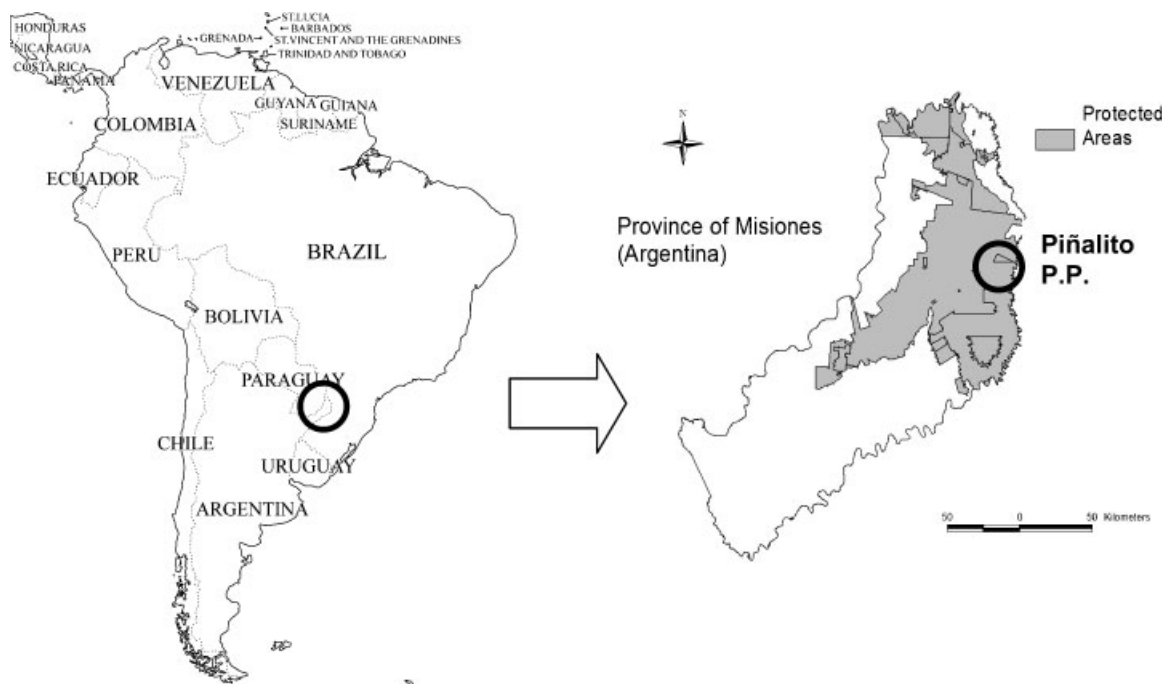


Fig. 1. Geographic location of the study area.

TABLE I. Age-Sex Composition of the Four Study Groups (BR1, BR2, BLG1, BLG2) 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
BLG1	1-2	5	1	0	0-2	4-5	1-3
BLG2	1-2	1	1	0-1	1	0-2	0-1

^aOne of the females was a black and gold howler adult female who migrated to 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.

groups of different species overlapped extensively in their home ranges, conspecific groups showed little or no overlap [Agostini et al., in press]. All four groups were previously habituated, and most of groups' members were identified individually by natural markings (scars, relative body sizes, and color patterns).

Food Availability Estimates

To estimate density, distribution, and abundance of plant resources available in the forest, in collaboration with two botanists (M. Srur and F. Gatti), we carried out a vegetation survey within the home ranges of the study groups. We selected 209 points (20 m apart) along transect lines and identified and measured, at each point, four trees ≥ 10 cm diameter at breast height (DBH) using the Point-Quarter method [Krebs, 1989]. Using this method, we sampled 1.1% of the area that included the home ranges of our four study groups. To estimate plant productivity, we established two phenological trails (total length = 6.65 km), partially crossing all four study groups' home ranges along two paths of the park, in which we selected 253 trees (with DBH ≥ 10 cm) of 40 tree species consumed by howlers [6.2 (± 2.6 SE) individuals per species on average; range: 1-11]. The list of food species was compiled on the basis of both our own preliminary data collected between January 2005 and November 2006 at the site and a literature review of the species consumed by BLG and BR [Aguiar et al., 2003; Bravo & Sallenave, 2003; Chiarello, 1994; Galetti et al., 1994; Miranda & Passos, 2004; Prates et al., 1990; Zunino, 1989]. Between December 2006 and November 2007, I. Agostini and I. Holzmann monitored the selected 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 [0 = 0%, 1 = 1-10%, 2 = 11-30%, 3 = 31-100%; see Placci, 1995]. The phenological scores of individual trees of each species were averaged to 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, we obtained a monthly Food Availability Index (FAI) by multiplying the PISp by the basal area (m^2/ha) obtained by the vegetation survey data [Zunino et al., 2001]. Finally, we calculated a monthly total FAI for each phenophase by adding FAI indices across all plant food species. For fruit availability estimates, we considered only fleshy ripe fruits because howlers fed mostly on ripe fruits. We excluded *Ficus* sp. (Moraceae), a species characterized by asynchronous fructification, which appeared to inflate measurements of fruit availability indices between May and August, as a result of a mismatch between what trees were sampled and what trees were actually available within a group's home range [Agostini, 2009]. For the index of conifer cone availability, we considered only male cones because we never observed howlers feeding on conifer female cones at our study site.

Feeding Data Collection

Between December 2006 and November 2007, I. Agostini and I. Holzmann, with the help of one or two field assistants at a time, followed each howler group during 3.02 (± 0.6 SD) days on average per month, totaling 308 hr of observation for BR1, 352 hr for BR2, 351 hr for BLG1, and 383 hr for BLG2. We collected data on feeding behavior using scan sampling [Altmann, 1974], at 10-min intervals, with scans lasting 3 min. Except for a few gaps, when howler groups were lost or out of view, scan sampling was continuous throughout the day, beginning as early as 0550 hr and finishing as late as 1930 hr, depending on season and on the monkeys' activity cycles. We always took a group scan if ≥ 1 individual came into view during the scan period. During scans, we watched each individual for 5 sec after it came into view and recorded its predominant activity. We tried to collect behavioral records on as many individuals as possible during a scan, by frequently changing position, and we deliberately avoided resampling the same subjects even in cases of uncertain subjects' identity. We scored a feeding record when an individual procured and/or handled food items with hands or mouth, as well as when it chewed and ingested food. We classified food types as: (1) ripe or unripe fruits, (2) mature or young leaves (including stems and petioles), (3) flowers or flower buds, (4) male pine cones, (5) bark, (6) other, and (7) undetermined. Fruit ripeness and leaf maturity were classified according to color, texture, and size, or in the absence of those data, it was scored as undetermined. We were able to identify most food items to the species level, at least for tree resources

[e.g., Agostini & Visalberghi, 2005; Di Bitetti, 2001]. We included “Unidentified Vines,” an important source of leaves for howlers, as an additional species in the analyses [see Agostini, 2009, for a discussion on the potential risk of inflating the apparent interspecific overlap by doing this]. All research reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and all research protocols were reviewed and approved by the Ministry of Ecology of the province of Misiones, Argentina. Moreover, all research reported in this manuscript complied with the protocols approved by the appropriate institutional Animal Care and Use Committee, and adhered to the legal requirements of Argentina in which the work took place.

Data Analyses

We calculated the proportion of feeding time howlers devoted to different food items, by dividing the number of feeding records for a particular food item by the total number of feeding records obtained during each scan. Then, for each monthly sample, we summed these proportions and divided by the number of scans obtained to control for differences in the number of scans between months.

The main study period was divided into 12 monthly samples (December 2006–November 2007). Because, for BR1 group, we almost entirely lacked the October sample, we lumped samples of September and October, and used the lumped values for comparisons with the other groups during both months. Most monthly samples were obtained within ten days of the two-day period of plant phenology monitoring, so that behavioral observations can be tightly correlated with the availability of food sources during the corresponding sample months.

We analyzed diet in terms of proportions of food types and specific food items (plant species and parts) obtained from the scan samples. Because these were never significantly different between individuals in conspecific groups, these data were averaged to be used in between-species comparisons. We calculated dietary overlap for specific food items among groups and between species by (1) summing the shared percentages of dietary components [Holmes & Pitelka, 1968], and (2) using the Morisita's index modified by Horn [1966], C_H , (range: 0–1, minimum and maximum overlaps, respectively). We used both overlap indices for comparability with other studies. Based on the proportions obtained by scan data, we estimated dietary diversity and evenness in the use of specific food items using the Shannon Diversity Index, H' and the Shannon Evenness Index, J (range: 0–1, complete unevenness and evenness, respectively) [Magurran, 2004].

We used non-parametric statistics because data were rarely normally distributed and variances were

typically heterogeneous even after transformations [Sokal & Rohlf, 1995]. All the statistical tests were two-tailed, with α set at 0.05, and were performed with Statistica software 5.5.

RESULTS

Food Availability

The availability of food in the home ranges of our howler study groups showed item-specific seasonal variations (Fig. 2). Although mature leaves were highly available throughout the year, young leaves were scarce during most of the cold season (April–August). Flowering showed a bimodal pattern, with the highest peak in August–September and a smaller one in February. Fleshy ripe fruits did not show any pronounced peak of availability across months, whereas male cones of *P. elliotii* and *A. angustifolia* were mostly available from June to August. We found only one correlation between monthly food availability and climatic variables that held statistically significant after applying the Bonferroni correction for multiple tests: young leaf availability was positively correlated with maximum monthly temperature ($r_s = 0.81$, $P = 0.001$).

Considering together monthly variation in the availability of young leaves, fruits, and flowers (resources commonly considered as high quality foods for howlers), we differentiated a “lean season” (May–August) and an “abundant season” (September–April) of low and high food availability, respectively [see Di Bitetti, 2001, for a similar classification approach in a study area close to this one]. During the lean season, the mean monthly amount of high-quality foods available to howler groups was 36% the mean monthly amount available in the abundant season.

Dietary Patterns: Species-Level Analysis

Overall, during the study period, BR devoted most of the feeding time to leaves (62%) and fruits (24%), and to a lesser extent to pine cones (7%) and flowers (6%). Similarly, BLG fed mostly on leaves (64%), followed by fruits (19%), the bark of *Eucalyptus* trees (7%), flowers (6%), and pine cones (3%). Over the year, both howler species fed almost equally on mature and young leaves (BR: 27% mature leaves and 24% young leaves; BLG: 26% mature leaves and 25% young leaves), and consumed consistently more ripe fruits than unripe ones (BR: 21% ripe, 2% unripe, and 2% undetermined fruits; BLG: 15% ripe, 4% unripe, and 1% undetermined fruits). During the lean season, both howler species significantly reduced fruit consumption (Mann–Whitney: $U_{4,8} = 3$, $P = 0.03$, for both BR and BLG), increasing the time spent feeding on mature leaves (BR: $U_{4,8} = 0$, $P = 0.006$; BLG: $U_{4,8} = 2$, $P = 0.017$) and pine cones ($U_{4,8} = 4$, $P = 0.041$, for both species) (Fig. 3). Both species consumed more

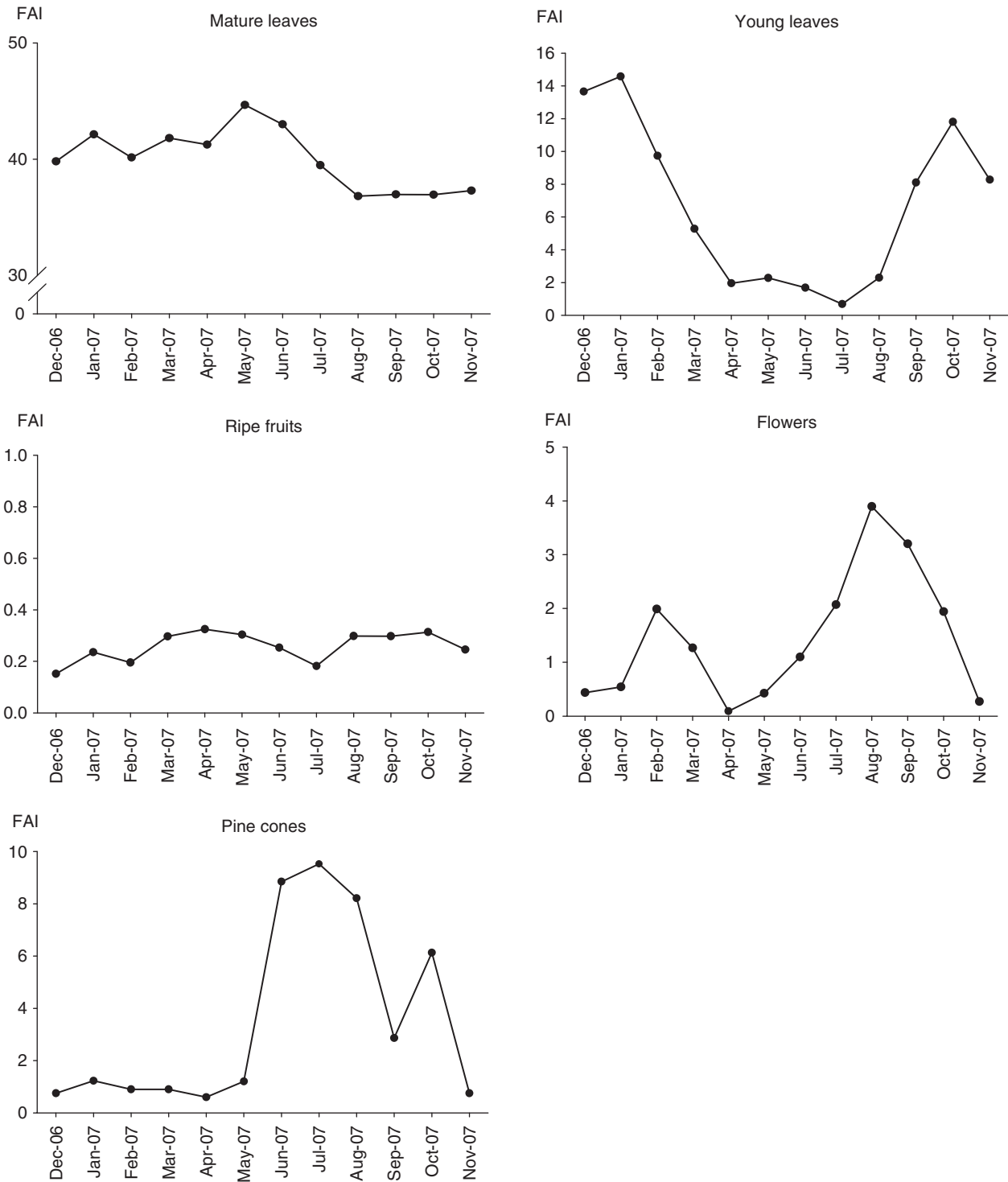


Fig. 2. Monthly variations of FAIs for mature leaves, young leaves, ripe fruits, flowers, and male pine cones during the study period. Y-axes are differently scaled for each graph. FAIs, Food availability Indices.

flowers in August–September, corresponding to the peak of tree flower availability, and in December–January, and only BLG (including the immigrant adult BLG female in the BR2 group) fed on the bark of *Eucalyptus* during most of the abundant season

(Fig. 3). Comparing monthly proportions of feeding time on different food types between species, we found that BLG ate significantly more unripe fruits (Wilcoxon: $t = 9$, $P = 0.033$) and bark ($t = 0$, $P = 0.005$) than BR.

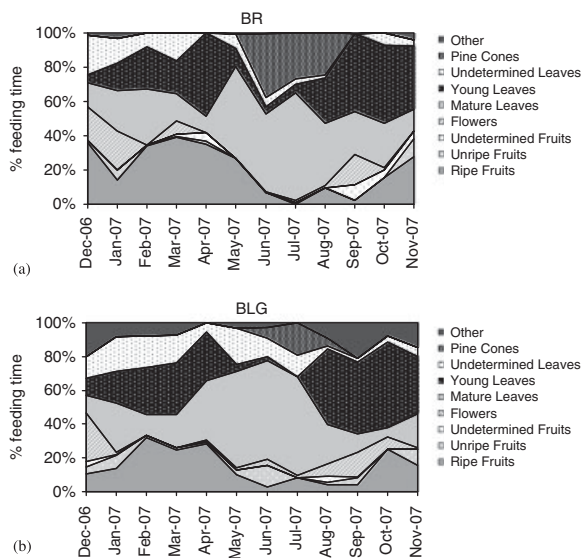


Fig. 3. Monthly diet of (a) brown howlers and (b) black and gold howlers in terms of percent of feeding time devoted to the main food types. The category “Other” includes bark and other minor food types.

Only for BLG, the time spent feeding on mature leaves showed a weak positive and marginally significant correlation with mature leaf availability across months ($r_s = 0.55$, $P = 0.06$). For both howler species, the time spent feeding on pine cones was positively correlated with pine cones availability across months (both howler species: $r_s = 0.76$, $P < 0.01$). Monthly proportions of other food types consumed by each howler species were not significantly correlated with their respective availability.

Vines, of which we could identify 13 species, provided the greatest proportion of foliage to the diet of both howlers' species (37% of feeding time for BR and BLG). Other major sources of foliage were tree species of Fabaceae like *Lonchocarpus campestris* and *Erythrina falcata*, which, in particular, provided young leaves between August and November. *P. elliotii* mature leaves were the most frequently consumed item by group BR1 in September–October, and the epiphyte *Phylodendron bipinnatifidum* (Araceae) was an important source of mature leaves for BLG at the beginning of the lean season, between April and June (Table II).

Ficus sp. was the most important ripe fruit source for both howlers (7% of feeding time for BR and BLG), especially from December to May. *Celtis* sp. (Ulmaceae) also provided an important ripe fruit source for BR between February and May. Ripe and unripe fruits of the palm *Syagrus romanzoffiana* (Arecaceae) were exclusively consumed by BLG, especially in May–June and November. Only BR fed on *Eucalyptus* sp. fruits, especially in April, June, August, and September. Male cones of *P. elliotii* were among the five highest-ranked items for BR for most of the lean season. Pine cones represented a small proportion of feeding time for BLG during the

same period. Major sources of flowers for both howlers were *Apuleia leiocarpa* (Fabaceae) and the vines *Arrabidaea* spp. and *Macfadenya uncatata* (Bignoniaceae), and, only for BR, *Eucalyptus* sp. Finally, the bark of *Eucalyptus* sp. was an important item only for BLG, especially in December–January and in August–September (Table II).

During the study period, BR consumed 97 specific food items (of which 29 were of exclusive use) from 40 plant species, and BLG consumed 144 specific food items (of which 76 were of exclusive use) from 56 plant species. Overall, BLG showed a diet significantly more diverse in terms of specific food items than BR across months (mean \pm SE Shannon diversity indices: $H' = 2.39 \pm 0.09$ for BR, and $H' = 2.77 \pm 0.08$ for BLG; Wilcoxon: $t = 0.0$, $P = 0.002$) (Fig. 4a). Moreover, although BR reduced significantly their dietary diversity during the lean season compared with the abundant season (Mann–Whitney: $U_{4,8} = 2.0$, $P < 0.017$), BLG did not show significant seasonal differences in their dietary diversity ($U_{4,8} = 15$, $P = 0.87$) (Fig. 4a).

The greater dietary diversity showed by BLG is explained by their higher richness in specific food items used compared with that of BR. In fact, the evenness component did not significantly differ between species across months (mean \pm SE Shannon evenness indices: $J = 0.78 \pm 0.02$ for BR, and $J = 0.82 \pm 0.01$ for BLG; Wilcoxon: $t = 21$, $P = 0.16$) (Fig. 4b). However, as observed for overall diversity, although BR reduced their dietary evenness during the lean season (Mann–Whitney: $U_{4,8} = 0.0$, $P = 0.007$), BLG's evenness in diet did not significantly change between seasons ($U_{4,8} = 7$, $P = 0.13$) (Fig. 4b).

On average, BR and BLG overlapped 45.64% (± 2.97 SE) in the use of specific food items across months (range: 28.70–64.08) by the Percentage Index, or 0.60 (± 0.05 SE) (range: 0.28–0.88) using the Morisita–Horn Index. Overlap did not vary significantly between seasons (Mann–Whitney: $U_{4,8} = 11$, $P = 0.40$, Fig. 5) and did not significantly correlate with monthly availability of any food type.

Dietary Overlap: Group-Level Analysis

Over the study period, monthly between-group percentage dietary overlap did not significantly vary intra- or interspecifically among all group pairs according to specific food items use (Friedman ANOVA: $\chi^2_{5,12} = 5.1$, $P = 0.40$) (Table III). Analyzing separately for the two seasons, we found that overlap in specific food items across all pairs of groups varied significantly, both in the abundant season ($\chi^2_{5,8} = 11.36$, $P = 0.045$) and in the lean season ($\chi^2_{5,4} = 11.29$, $P = 0.046$). However, in both seasons, we did not find any consistent pattern indicating higher or lower overlap of conspecific groups relative to groups of different species, nor of groups sharing large parts of their home range relative to spatially separated groups (Table III).

TABLE II. Monthly Top Five Ranked Specific Food Items Consumed (Percentages of Feeding Time) by Brown Howlers (BR) and Black and Gold Howlers (BLG) During the Study Period

BR (December 2006)		BLG (December 2006)	
<i>Ficus</i> sp. (RFr)	31.00%	<i>Eucalyptus</i> sp. (B)	19.40%
<i>Fridericia</i> sp. (FL)	15.00%	<i>Fridericia corallina</i> (FL)	12.42%
Unidentified vines (UndL)	7.56%	<i>Fridericia</i> sp. (FL)	9.91%
Unidentified vines (ML)	7.13%	<i>Ficus</i> sp. (RFr)	7.69%
<i>Acacia</i> sp. (UndL)	6.47%	Unidentified vines (UndL)	6.55%
BR (January 2007)		BLG (January 2007)	
<i>Eucalyptus</i> sp. (FL)	21.15%	Unidentified vines (UndL)	18.75%
<i>Phytolacca dioica</i> (RFr)	12.53%	Unidentified vines (ML)	14.40%
Unidentified vines (ML)	10.72%	<i>Phytolacca dioica</i> (RFr)	6.97%
Unidentified vines (UndL)	6.88%	<i>Eucalyptus</i> sp. (B)	6.52%
<i>Lonchocarpus campestris</i> (YL)	6.06%	<i>Ficus</i> sp. (RFr)	6.52%
BR (February 2007)		BLG (February 2007)	
<i>Nectandra lanceolata</i> (RFr)	19.45%	<i>Lonchocarpus campestris</i> (YL)	14.46%
<i>Pinus elliottii</i> (ML)	15.46%	<i>Phytolacca dioica</i> (RFr)	12.33%
<i>Lonchocarpus campestris</i> (YL)	14.41%	Unidentified vines (UndL)	11.03%
<i>Acacia</i> sp. (ML)	11.49%	Unidentified vines (YL)	7.05%
<i>Celtis</i> sp. (RFr)	8.21%	<i>Nectandra lanceolata</i> (RFr)	6.40%
BR (March 2007)		BLG (March 2007)	
<i>Celtis</i> sp. (RFr)	22.15%	<i>Acacia</i> sp. (YL)	15.70%
<i>Acacia</i> sp. (UndL)	12.08%	Unidentified vines (ML)	12.57%
<i>Ficus</i> sp. (RFr)	11.88%	Unidentified vines (YL)	10.49%
<i>Eucalyptus</i> sp. (FL)	8.09%	<i>Celtis</i> sp. (RFr)	10.25%
Unidentified vines (ML)	7.71%	Unidentified vines (UndL)	9.11%
BR (April 2007)		BLG (April 2007)	
<i>Ficus</i> sp. (RFr)	24.77%	Unidentified vines (ML)	20.15%
Unidentified vines (YL)	22.38%	<i>Ficus</i> sp. (RFr)	18.60%
<i>Acacia</i> sp. (YL)	22.00%	Unidentified vines (YL)	16.32%
<i>Eucalyptus</i> sp. (UFR)	5.17%	<i>Acacia</i> sp. (YL)	12.50%
<i>Prunus</i> sp. (RFr)	5.17%	<i>Phylodendron bipinnatifidum</i> (ML)	6.78%
BR (May 2007)		BLG (May 2007)	
Unidentified vines (ML)	39.81%	Unidentified vines (ML)	19.67%
<i>Ficus</i> sp. (RFr)	13.67%	<i>Phylodendron bipinnatifidum</i> (ML)	12.66%
<i>Celtis</i> sp. (RFr)	7.91%	Unidentified vines (UndL)	11.86%
<i>Acacia</i> sp. (YL)	5.33%	<i>Ficus</i> sp. (ML)	7.94%
Unidentified vines (UndL)	5.13%	<i>Syagrus romanzoffianum</i> (RFr)	4.04%
BR (June 2007)		BLG (June 2007)	
<i>Pinus elliottii</i> (PC)	37.52%	Unidentified vines (ML)	22.88%
Unidentified Vines (ML)	24.85%	<i>Phylodendron bipinnatifidum</i> (ML)	20.61%
<i>Acacia</i> sp. (ML)	10.30%	<i>Syagrus romanzoffiana</i> (UFR)	7.70%
<i>Ficus</i> sp. (ML)	5.41%	<i>Pinus elliottii</i> (PC)	6.22%
<i>Eucalyptus</i> sp. (RFR)	4.55%	<i>Ficus</i> sp. (UndFr)	4.86%
BR (July 2007)		BLG (July 2007)	
Unidentified vines (ML)	28.65%	Unidentified vines (ML)	28.66%
<i>Pinus elliottii</i> (PC)	26.88%	<i>Pinus elliottii</i> (PC)	19.11%
<i>Acacia</i> sp. (ML)	22.32%	<i>Acacia</i> sp. (ML)	11.04%
Unidentified trees (ML)	6.90%	<i>Celtis</i> sp. (ML)	10.47%
<i>Machaerium stipitatum</i> (ML)	2.96%	Unidentified vines (UL)	6.97%
BR (August 2007)		BLG (August 2007)	
<i>Pinus elliottii</i> (PC)	24.51%	Unidentified vines (YL)	15.80%
Unidentified vines (ML)	22.92%	Unidentified vines (ML)	15.22%
<i>Eucalyptus</i> sp. (RFR)	9.43%	<i>Lonchocarpus campestris</i> (YL)	10.56%
<i>Erythrina falcata</i> (YL)	8.18%	<i>Eucalyptus</i> sp. (B)	8.17%
Unidentified vines (YL)	5.99%	<i>Pinus elliottii</i> (PC)	4.73%
BR (September 2007)		BLG (September 2007)	
<i>Pinus elliottii</i> (ML)	19.11%	<i>Eucalyptus</i> sp. (B)	18.22%
<i>Erythrina falcata</i> (YL)	13.09%	<i>Erythrina falcata</i> (YL)	10.86%
<i>Apuleia leiocarpa</i> (FL)	12.05%	<i>Apuleia leiocarpa</i> (FL)	10.68%
<i>Eucalyptus</i> sp. (UFR)	9.18%	Unidentified vines (ML)	5.74%
Unidentified vines (YL)	8.09%	<i>Celtis</i> sp. (YL)	5.64%

TABLE II. Continued

BR (October 2007)		BLG (October 2007)	
<i>Pinus elliottii</i> (ML)	19.11%	<i>Ficus</i> sp. (RFr)	19.57%
<i>Apuleia leiocarpa</i> (YL)	15.71%	<i>Dalbergia frutescens</i> (YL)	14.17%
Unidentified vines (YL)	11.50%	Unidentified vines (YL)	10.37%
<i>Acacia</i> sp. (YL)	9.02%	<i>Erythrina falcata</i> (YL)	10.28%
<i>Erythrina falcata</i> (YL)	8.22%	<i>Macfadenya uncata</i> (FL)	6.39%
BR (November 2007)		BLG (November 2007)	
<i>Lonchocarpus campestris</i> (YL)	22.89%	<i>Lonchocarpus campestris</i> (YL)	24.44%
<i>Prunus</i> sp. (RFr)	19.36%	<i>Eucalyptus</i> sp. (B)	14.53%
<i>Ocotea puberula</i> (UFr)	10.36%	<i>Ocotea puberula</i> (UFr)	7.65%
<i>Campomanesia xanthocarpa</i> (RFr)	6.57%	<i>Prunus</i> sp. (RFr)	6.78%
<i>Acacia</i> sp. (YL)	5.03%	<i>Syagrus romanzoffiana</i> (RFr)	6.54%

FL, flowers; ML, mature leaves; YL, young leaves; UndL, undetermined leaves; RFr, ripe fruits; UFr, unripe fruits; UndFr, undetermined fruits; PC, pine cones; B, bark.

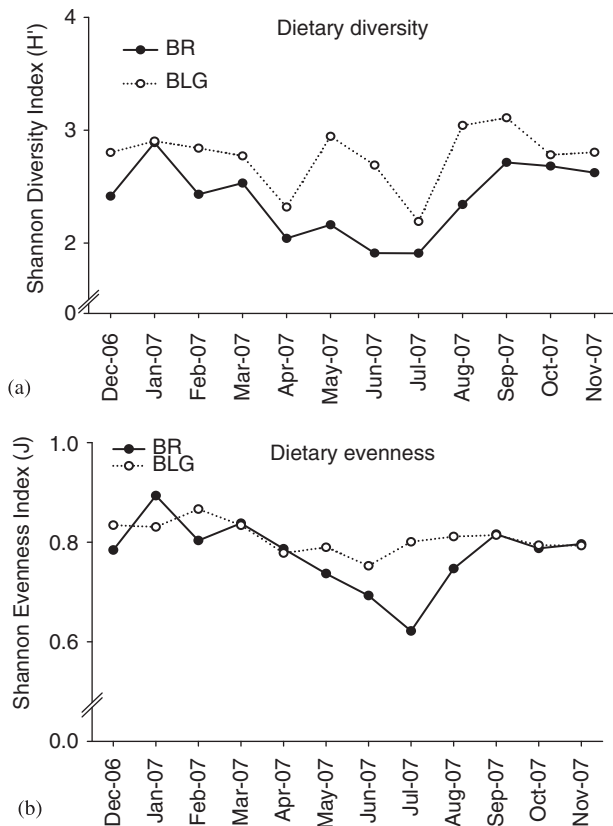


Fig. 4. Monthly values of the Shannon index of (a) diversity and (b) evenness in specific food items use for brown howlers (black circles, continuous lines) and black and gold howlers (white circles, dotted lines).

DISCUSSION

Diet: Interspecific Similarities and Differences

In general, at our study site, groups of the same species shared similar dietary profiles. In addition, evidence from our study populations of BR and BLG

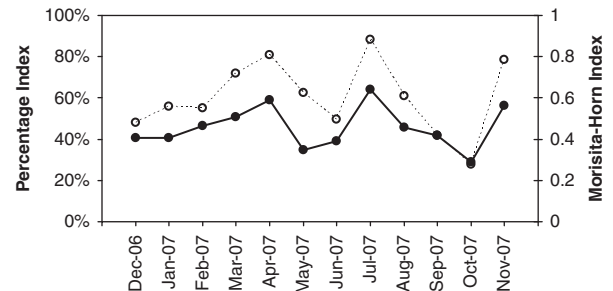


Fig. 5. Monthly specific food items overlap between brown howlers and black and gold howlers calculated by the Percentage Index (black circles and solid line) and the Morisita-Horn Index (white circles and dotted line).

[Agostini, 2009], as well as from other populations [Koch & Bicca-Marques, 2007; Prates & Bicca-Marques, 2008], indicates that different age-sex classes within groups show no difference in the consumption of major food types, thus reducing any source of further intraspecific variation in the diet.

Both BR and BLG at El Piñalito showed similar dietary profiles, feeding extensively on leaves and fruits, and to a lesser extent on flowers and other items, thus being classifiable as folivores-frugivores like all other howler populations [Crockett & Eisenberg, 1987; Di Fiore & Campbell, 2007]. Given the limited physiological adaptations to folivory, howlers are reported to selectively consume greater amounts of young, easier to digest leaves, with a higher protein to fiber ratio [Milton, 1980] and lower concentrations of plant secondary compounds [Glander, 1978] compared with mature leaves during most of the year [Crockett & Eisenberg, 1987]. However, similar to what has been found in several other studies [reviewed in Bicca-Marques, 2003], at El Piñalito, both howler species devoted equal amounts of their feeding time to mature leaves and young leaves. In the abundant season, young leaves were used more extensively (BR = BGL: 30%) than mature leaves (BR: 20%; BLG: 18%). However, in the lean season, the consumption of mature leaves (BR: 50%;

TABLE III. Monthly Percentage Indices of Overlap in the Use of Specific Food Items for Each Pair of Howler Groups

Month	BR–BR	BLG–BLG	BR–BLG			
	BR1–BR2	BLG1–BLG2	BR1–BLG2	BR2–BLG1	BR1–BLG1	BR2–BLG2
December 2006	26.5%	36.2%	29.2%	19.0%	46.7%	23.9%
January 2007	18.5%	52.4%	31.5%	34.9%	29.3%	32.4%
February 2007	23.9%	26.1%	18.1%	40.3%	27.4%	38.3%
March 2007	42.6%	44.2%	38.4%	58.2%	40.9%	35.5%
April 2007	25.0%	26.8%	39.0%	58.2%	45.9%	10.4%
May 2007	39.6%	30.9%	30.6%	24.8%	31.0%	36.5%
June 2007	49.5%	41.6%	37.7%	24.3%	25.8%	48.9%
July 2007	65.9%	28.2%	53.9%	50.0%	39.1%	62.7%
August 2007	59.8%	47.4%	46.3%	42.7%	39.2%	37.4%
September 2007	32.6%	38.1%	28.9%	35.8%	21.7%	25.9%
October 2007	20.5%	38.3%	18.7%	25.2%	27.1%	19.7%
November 2007	45.9%	46.4%	40.9%	42.2%	59.5%	49.2%
Mean	37.5%	38.0%	34.4%	38.0%	36.2%	35.1%
SD	15.6%	8.7%	10.5%	13.2%	11.0%	14.2%

BR–BR and BLG–BLG indicate conspecific pairs of brown howler and black and gold howler groups, respectively; BR–BLG indicates heterospecific pairs of brown howler and black and gold howler groups.

BLG: 49%) greatly exceeded that of young leaves (BR: 11%; BLG: 13%). Seasonal changes in dietary profile by both howler species is likely to reflect monthly availability of leaves as a food resource (Fig. 2).

As reported for other howler species [Crockett & Eisenberg, 1987], both BR and BLG at El Piñalito consumed ripe fruits more than unripe ones, especially during the abundant season. However, BLG consumed significantly more unripe fruits than did BR. Waser [1987] argued that species that eat immature fruits could adversely affect a sympatric species that feed on the same fruits when ripe, making exploitation competition possibly one-sided. Thus, if fruits are a limiting resource, BR could be more adversely affected by the exploitation competition through preemption by black howlers. Finally, both howlers relied on *Ficus* sp. as the main fruit source during many months of the year, supporting the general idea that *Ficus* constitutes one of the primary fruit resources for howlers throughout their distribution [Crockett & Eisenberg, 1987].

Although the consumption of seasonal items, such as young leaves, fruits, and flowers, varied between seasons, howlers did not consume these items according to their availability. Foraging theory (prey model) predicts that depending on the profitability of a food type (i.e., energy content per unit handling time), a forager may not consume food items based solely on availability. A particular food item could become more important in the diet when it is scarcer, simply because it becomes more profitable relative to other food items available at that time [Stephens & Krebs, 1986]. In addition, during periods of high food abundance, a resource at its peak of availability may provide more food than the

howlers require. Thus, peak consumption is not always expected to coincide with peak productivity. Further, the lack of correlation between food items availability and consumption constitutes an evidence of howlers' feeding selectivity, as reported by other authors [Glander, 1981; Milton, 1980].

BR and BLG at our site showed some differences in specific items that were exclusively or preferentially used. Some of these items may have been important resources (among the top five ranked) to each howler species during times of low food availability, such as fruits and flowers of exotic *Eucalyptus*, for BR. During the lean season, other exotic food sources, such as pine cones of *P. elliotii*, constituted important food sources for both howler species, and represented staple foods [sensu Milton, 1980; i.e., food species that are eaten for more than 20% of feeding time during more than 1 month] for BR. The use of exotic plants, during periods of food shortages, has been reported for BR in a disturbed subtropical forest by Miranda and Passos [2004] and for BLG in a semi-natural forest by Bicca-Marques and Calegare-Marques [1994a,b]. Among the BLG's most preferred foods, at the start of the lean season, were mature leaves of the epiphyte *P. bipinnatifidum* and fruits of the palm *S. romanzoffiana*. Especially, the latter has been shown to be a food source for BLG in other studies [Bicca-Marques & Calegare-Marques, 1994a; Kowalewski, 2007]. Curiously, in contrast with several studies in which *S. romanzoffiana* is included in BR's diet [Aguar et al., 2003; Chitolina & Sander, 1981; Galetti et al., 1994; Miranda & Passos, 2004] at our study site, BR groups, which included several palm trees (density: 6.0 individuals/ha) within their home ranges, were never observed feeding on them. Finally, BLG

consumed the bark of *Eucalyptus*, during most of the abundant season at our study site. Bark feeding was reported for BLG also by Bicca-Marques and Calegario-Marques [1994a,b].

At El Piñalito, BR and BLG, studied at the same time and in the same area, showed differences in their dietary diversity. BLG's monthly diet was significantly more diverse than BR's in terms of specific food items consumed. BLG's greater dietary breadth could reflect their large ecological flexibility and the fact that they inhabit the southernmost distribution of any howler species [Cowlshaw & Dunbar, 2000].

Trophic Overlap

Overall, at El Piñalito, the dietary overlap between syntopic BR and BLG was among the highest compared with many other primate species pairs studied in sympatry (with the notable exceptions of some *Saguinus* species pairs and *Cercopithecus* species pairs; Table IV). Most of these studies have focused on species that are sympatric across broad areas of their ranges. These species, although sharing many food items, usually either broadened their diet or switched to different food sources during periods of food scarcity [Chapman, 1987; Cords, 1987; Stevenson et al., 2000; Terborgh,

1983]. In some cases, it has been argued that these seasonal shifts in diet were the result of feeding competition. In other cases, it has been argued that during food limited periods of the year different species have behavioral and morphological adaptations that aid them in exploiting alternative types of fallback foods [Lambert, 2007; Marshall & Wrangham, 2007]. In contrast, Stevenson et al. [2000] found that woolly monkeys (*Lagothrix lagotricha*) and spider monkeys (*Ateles belzebuth*), two ecologically similar species rarely found sympatrically, showed the highest monthly average fruit diet overlap compared with the other primate species coexisting at their study site. These two species did not show any significant variation in their diet breadth and overlap in the period of fruit shortage. At El Piñalito, the monthly average overlap between BR and BLG was higher than that found for woolly monkeys and spider monkeys (Table IV), and monthly overlap did not vary significantly between seasons or in response to food availability. Moreover, we found similar inter- and intraspecific dietary overlap among howler groups throughout the year. Differences found seasonally in between-groups dietary overlap did not indicate any consistent pattern of lower overlap between groups of different species compared with conspecific groups. We cannot rule out the possibility that, at our site, resource availability

TABLE IV. Annual and/or Monthly/Seasonal Mean (Range) Overlap Values (Percentage or Morisita-Horn Indices) in the Use of Plant Specific Food Items Between Pairs of Closely Related Primate Species

Species	Annual overlap	Monthly/seasonal mean overlap (range)	Study site	Source
<i>Cercopithecus campbelli</i> vs. <i>C. diana</i>	51%	39% (12–58)	Tai, Ivory Coast	Buzzard [2006]
<i>Cercopithecus campbelli</i> vs. <i>C. petaurista</i>	34%	26% (15–36)		
<i>Cercopithecus petaurista</i> vs. <i>C. diana</i>	37%	28% (11–37)		
<i>Cercopithecus nictitans</i> vs. <i>C. diana</i>	–	70%	Tai, Ivory Coast	Eckardt and Zuberbühler [2004]
<i>Cercopithecus mitis</i> vs. <i>C. ascanius</i>	70%	62% (53–74)	Kakamega, Kenya	Cords [1986]
<i>Cercopithecus mitis</i> vs. <i>C. ascanius</i>	34%	34% (5–55)	Kibale, Uganda	Struhsaker [1978]
<i>Colobus guereza</i> vs. <i>Procolobus badius</i>	–	7.1% (2–15.7)	Kibale, Uganda	Struhsaker and Oates [1975]
<i>Colobus guereza</i> vs. <i>Procolobus badius</i>	–	37.3%; 43.2%	Kibale, Uganda	Chapman et al. [2002]
<i>Colobus angolensis</i> vs. <i>C. guereza</i>	–	28.5% (14–38.7)	Ituri Forest, Congo	Bocian [1997]
<i>Eulemur fulvus</i> vs. <i>E. rubriventer</i>	44%	43% (7–66)	Ranomafana NP, Madagascar	Overdorff [1993]
<i>Cebus apella</i> vs. <i>C. albifrons</i>	25%	–	Manu NP, Peru	Calculated from Terborgh [1983]
<i>Saguinus imperator</i> vs. <i>S. fuscicollis</i>	43%	–		
<i>Saguinus mystax</i> vs. <i>S. fuscicollis</i>	86.5%	–	Amazonian Peru	Castro [1991]
<i>Lagothrix lagotricha</i> vs. <i>Ateles belzebuth</i>	–	0.35 ^{a,b}	Tinigua NP, Colombia	Stevenson et al. [2000]
<i>Lagothrix lagotricha</i> vs. <i>Ateles belzebuth</i>	27% ^b	–	Yasuni NP, Ecuador	Dew [2005]
<i>Alouatta guariba</i> vs. <i>A. caraya</i>	59.36%	45.64% (28.7–64.08)	El Piñalito PP, Northeast Argentina	This study
	0.79 ^a	0.6 (0.28–0.88) ^a		

^aOverlaps are calculated by the Morisita-Horn index. All other references measured overlap by summing shared percentages of resource use (Holmes and Pitelka Index).

^bOverlaps estimated for the fruit component of diet.

for howlers during the lean season was not low enough to create a strong competitive regime between the species, and this may explain the lack of seasonal changes in resource overlap. Finally, we did not find any evidence of interspecific contest competition between BR and BLG at our study site, given that, throughout the year, encounters between groups of different species were consistently more pacific than encounters between conspecific groups, regardless of context [Agostini et al., in press].

Our findings (high interspecific dietary overlap throughout the year and similar degrees of inter- and intraspecific dietary overlap) are in strongest agreement with the predictions of our third hypothesis, which states that syntopic BR and BLG are ecologically equivalent and exploit highly similar resources. The few interspecific differences we found, such as eucalyptus bark feeding, increased dietary diversity and unripe fruit feeding in BLG and increased use of pine cones and eucalyptus flowers and fruits in BR, suggest that each species is adapted to slightly different ecological regimes (BLG = opportunistic forager in more seasonal and secondary forests; BR = more adapted to mature forests). Given their narrow area of coexistence and their similarity in dietary patterns, these two howler species have the potential to compete for food resources when found in sympatry. The low densities of both species at our study site (BR: 10 ind/km²; BLG: 15 ind/km²) when compared with other sites where they live alone [BR: median (range) = 20 ind/km² (0.6–113.4), *N* = 23 sites; data reviewed in Ingberman et al., 2009; BLG: median (range) = 50 ind/km² (3–425), *N* = 9 sites; data by Bravo & Sallenave, 2003; Dvoskin et al., 2004; Rumiz, 1990; and data reviewed in Henriques & Cavalcante, 2004] is consistent with two theoretical possibilities. One that these species may be competing for resources and negatively affecting each other's population growth. Alternatively, it may be that areas where both species range overlaps represent a set of ecological conditions that are not highly favourable to either species. At present, we do not have direct evidence for interspecific competition in these howler species. Moreover, other factors (e.g., recent yellow fever epidemics) may have a stronger negative effect on howler population density at our site. Nevertheless, we conclude that high levels of niche overlap among different howler species may play an important ecological role maintaining their parapatric distribution throughout the Neotropics.

ACKNOWLEDGMENTS

We thank the Ministry of Ecology of Misiones for the research permit, D. Colcombet for facilitating accommodations at the field site, and park rangers

for their support during the study. We are grateful to the 24 field assistants who helped us in the data collection and other field activities. In particular, the field work would have been impossible without the hard work and long-term commitment of E. Pizzio, N. Areta, B. Ripoll, M. Brivodoro, R. Pfoh, V. Orosa, D. Muñoz, and E. Acevedo. We thank M. Srur and F. Gatti for their help in the vegetation survey and identification of plants. C. H. Janson, E. Visalberghi, J. C. Bicca-Marques, and an anonymous reviewer provided helpful comments on this manuscript. All research reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and all research protocols were reviewed and approved by the Ministry of Ecology of the province of Misiones, Argentina. Moreover, all research reported in this manuscript complied with the protocols approved by the appropriate institutional Animal Care and Use Committee, and adhered to the legal requirements of Argentina, in which the work took place.

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