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Influence of seasonality, group size, and presence of a congener on activity patterns of howler monkeys

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Ecologically similar and closely related species in sympatry may differ in their activity patterns to avoid interspecific contest competition. We here present the 1st study aimed at evaluating the effects of seasonality, group size, and presence of a congener on the activity patterns of 2 syntopic species of howler monkeys, the brown howler (*Alouatta guariba clamitans*) and the black-and-gold howler (*A. caraya*), in northeastern Argentina. During 12 months, we collected activity data on 2 groups of each species characterized by different sizes and degrees of home-range overlap, together with data on food availability. We analyzed seasonal variation in activity budgets and daily activity patterns, as well as the relationships between monthly activity budget and food availability, diet, and climate, both within and between species. Black-and-gold howlers, more clearly than brown howlers, adopted an energy-minimization strategy, reducing costly activities such as moving and traveling, during the lean season. Within each howler species, individuals in the largest group showed a greater proportion of time spent moving or traveling, or both, compared to individuals in the smallest group, suggesting the existence of within-group food competition. Juveniles of both species rested less and moved and socialized more than adults. Overall, black-and-gold howlers spent proportionately more time moving and traveling, and less time resting, probably due to their larger mean group size, than brown howlers. Daily feeding peak times diverged only slightly among groups in the lean season, but differences between groups of different species with overlapping home ranges were not larger than those among scarcely or nonoverlapping groups (of same or different species). In conclusion, even though the 2 howler species showed differences in activity patterns, mainly related to differences in their response to food seasonality, and in group size, we found no evidence of time partitioning.

Key words: *Alouatta caraya*, *Alouatta guariba clamitans*, energy minimization, interspecific competition, time budget, time partitioning

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Animals have to deal on a daily basis with the challenge of balancing the time allocated into all the activities necessary for their self-maintenance and reproduction (Dunbar 1992). The time needed for most of the time-budget components (i.e., feeding, moving, resting, and social interactions) is a function of habitat-specific ecological conditions or the competitive regimes, or both, the animal faces (Caraco 1979; Dunbar et al. 2009). A number of mammalian studies have shown that species regulate their time budget in response to variation of environmental factors, such as climate and food quality, abundance, and spatiotemporal distribution (rodents—Cox and Hunt 1992, ungulates—Owen-Smith 1994, 1998, carnivores—Williams et al. 1997; Zielinski 2000, and primates—Clutton-Brock 1977a; Hanya 2004; Robinson 1986; Watts 1988; Zhou et al. 2007) and their specific responses to seasonality may vary according to their diet and physiology (Milton 1980; Zielinski 2000).

Time budgets of animals also are strongly influenced by sociodemographic factors, such as group size and composition (Caraco 1979; Pulliam 1973). For social mammals, such as primates, most socioecological models have proposed 2 major determinants of group size: the risk of predation, which puts a lower limit to group size and promotes group living, and within-group feeding competition, which sets the upper limit of group size by increasing costs of travel in larger groups (Chapman et al. 1995; Janson and Goldsmith 1995; van Schaik 1989). Specifically, as group size increases, the amount and quality of food available per capita within a food patch decreases, leading to higher levels of within-group feeding competition (Isbell 1991; Janson and Goldsmith 1995; van Schaik et al. 1983). Thus, individuals in large groups tend to increase the time spent traveling (i.e., the foraging effort) in order to fulfill their energetic requirements, and tend to decrease the time spent resting (Clutton-Brock and Harvey 1977; Janson and Goldsmith 1995; van Schaik et al. 1983; Wrangham et al. 1993). Feeding time may or may not increase with group size (Caraco 1979; Isbell and Young 1993; Janson and Goldsmith 1995; van Schaik et al. 1983), because larger groups frequently compensate for the costs of within-group competition by using other strategies such as traveling further per day, feeding on larger patches, or increasing group spread while feeding (Janson and Goldsmith 1995; Overdorff 1996). Further, because individuals may have different energetic demands according to age, sex, and reproductive condition, time allocation patterns may vary among individuals within groups (Clutton-Brock 1977a; Muruthi et al. 1991; Strier 1987). Finally, the presence of an ecologically and morphologically similar closely related species may promote differentiation in the use of time resource (i.e., temporal partitioning) to avoid interspecific competition (Carothers and Jaksic 1984; Schoener 1974), as shown for several mammalian species (rodents—Kronfeld-Schor and Dayan 2003, carnivores—Di Bitetti et al. 2009, 2010, and primates—Overdorff 1996; Singh et al. 2000; Sussman 1974; Wright 1989).

Primates represent a well-studied mammalian taxon. Although the effects of seasonality, group size, and presence of a congener on activity patterns have been studied separately in many primate species (e.g., Ganzhorn 1988; Hill et al. 2003; Isbell and Young 1993; Janson and Goldsmith 1995; Strier 1987; Sussman 1974; Wright 1989), the simultaneous analysis of these 3 variables and their interaction has been rarely tackled for any species (but see Overdorff 1996). Moreover, although most comparative primate studies on congeners have been focused on species pairs with large-scale sympatry, very little is known about parapatric species pairs when they occasionally co-occur in narrow contact zones (Bocian 1997; Stevenson et al. 2000).

In this paper we present results of the 1st study on the effects of seasonality in food availability, diet, and climate; group size and composition; and presence of a congener on the activity patterns of 2 syntopic species of howler monkeys, the brown howler (*Alouatta guariba clamitans*) and the black-and-gold howler monkey (*A. caraya*), in a contact zone lying in the Atlantic Forest of northeastern Argentina. These 2 species overlap considerably in their diet and use of space throughout the year, indicating a high potential for interspecific competition (Agostini et al. 2010a, 2010b).

Given their diet that is rich in highly fibrous and low-energy foods, such as leaves, and the lack of extreme physiological adaptations to folivory, howlers usually adopt behaviors that reduce energy expenditure according to the degree of leaf consumption (Milton 1980, 1998). This ecological strategy is classified as energy minimization (Milton 1980; Strier 1992). If howlers are indeed energy-minimizers, both howler species at our site should be expected to increase the percent time spent resting and decrease the time spent moving and traveling during seasonal shortages of high-quality foods (i.e., items relatively high in sugars or proteins and low in fibers or secondary compounds, or both, such as fleshy fruits, young leaves, and flowers—Milton 1980, 1981); as consumption of low-quality food (mature leaves) increases and that of high-quality food decreases; and under extremely low as well as high temperatures (i.e., resting and moving or traveling time budgets will show, respectively, negative and positive curvilinear relationships with temperature). Because of their high feeding selectivity, it is likely that howler food resources are patchy and in limited supply (Chiarello 1994; Milton 1980; for our study site: Agostini et al. 2010a) and thus their group size may be ecologically constrained by within-group scramble-feeding competition (Chapman et al. 1995; Chapman and Chapman 2000; Janson and Goldsmith 1995). If howlers experience the costs of within-group scramble-feeding competition, we expect individuals in larger groups to spend proportionately less time resting; to allocate more time traveling or moving (e.g., an increase in moving time within a patch—see Klein 1972), assuming that individual efficiency in exploiting a patch is reduced when the group is larger (Janson and van Schaik 1988); and to spend an equal or greater percentage of time feeding compared to individuals in smaller groups. Finally, given that in the study area groups of different species show a great overlap in diet (Agostini et al. 2010a) and space (Agostini et al. 2010b) throughout the year and could potentially compete for resources, we predict that the most range-overlapping groups of brown howlers and black-and-gold howlers (i.e., groups that overlap the most in their home ranges and core areas) will exhibit more divergent daily feeding peak times than the least (or not) range-overlapping groups, especially in the period of food shortage, when the potential effect of food competition is likely to be manifested.

Materials and Methods

Study species.—Species of howler monkeys (*Alouatta*) have an essentially parapatric distribution throughout the Neotropics, with a few narrow contact zones where species pairs are sympatric and occasionally syntopic, that is, co-occurring and overlapping their ranges in the same habitat within a zone of sympatry (Cortés-Ortiz et al. 2003; Groves 2001). For example, the only known contact zones between brown howlers (*A. g. clamitans*) and black-and-gold howlers (*A. caraya*) lie in the Atlantic Forest of Misiones Province in northeastern Argentina (Agostini et al. 2008; Di Bitetti 2003)

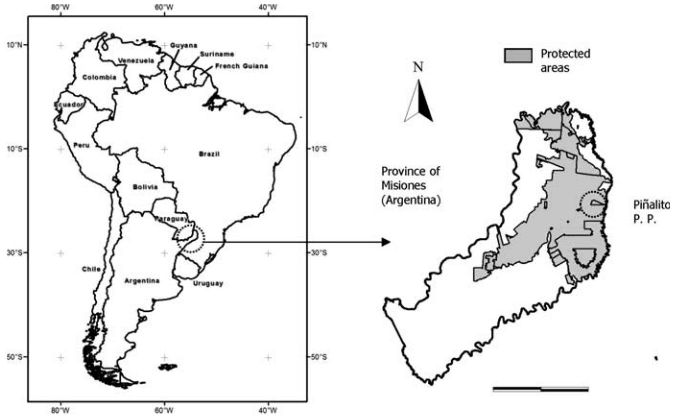

FIG. 1.—Map of the study site.

and in ecotonal areas between the Cerrado and the Atlantic Forest in southern Brazil (Aguiar et al. 2007; Bicca-Marques et al. 2008). Brown howlers are endemic to the Atlantic Forest of South America (Kinzey 1982), whereas black-and-gold howlers typically inhabit forests of the Cerrado, Pantanal, and Chaco ecoregions (Rumiz 1990). Both species have similar body masses but differ in their range of mean group sizes across different sites (brown howlers: 5.8–7.0; black-and-gold howlers: 6.4–18.5 [reviewed by Di Fiore and Campbell 2007]). Howler monkeys are strictly diurnal folivore–frugivores (Crockett and Eisenberg 1987) and have been classified as energy-minimizers (Milton 1980; Strier 1992), showing behavioral (e.g., long periods of inactivity and heat-conserving or heat-dissipating body postures) rather than physiological adaptations to folivory (Milton 1980, 1998).

Study site and subjects.—This study took place between December 2006 and November 2007 in El Piñalito Provincial Park (26°30′S, 53°50′W), a 3,796-ha strictly protected area within the Atlantic Forest of Misiones, in northeastern 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 19.8°C (±1.1°C *SE*). A cold season with shorter days occurred between May and August (average temperature: 15.1°C ± 0.8°C; average day length: 10.6 h ± 0.2 *SE*), whereas the rest of the year was warmer (22.2°C ± 0.5°C) with more hours of daylight (12.6 ± 0.3 h). Rainfall totalled 1,952 mm, with no marked seasonal pattern. Climatic data were provided by the Argentinean National Meteorological Service at Irigoyen, located approximately 40 km from our study site.

At the relatively high elevation of El Piñalito (~750 m above sea level), 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 small portions of secondary forest, 92 ha of old monospecific plantations of exotic pines (*Pinus elliottii*), several trees of exotic *Eucalyptus* sp., and 6 ha of native *Araucaria* plantation. Hunting pressure on monkeys is minimal or absent in the area.

TABLE 1.—Age–sex composition of the 4 study groups (brown howlers: BR1, BR2; black-and-gold howlers: BL1, BL2) during the study period. ADM = adult male; ADF = adult female; SBM = subadult male; SBF = subadult female; JVM = juvenile male; JVF = juvenile female; INF = infants of both sexes.

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	1–2	0–1

[a] One of the females was a black-and-gold howler adult female who migrated into the BR2 group before the beginning of the study period.

At this site, black-and-gold howler groups were larger than brown howler groups ($\bar{X} \pm SD$ for all groups censused in the study area; brown howlers: 4.83 ± 2.23, $n = 6$; black-and-gold howlers: 9.33 ± 3.21, $n = 3$; *t*-test: $t = -2.50$, $P = 0.041$). We collected data 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 ($n = 6$–7; Table 1). The 4 study groups occupied a total area of 165 ha including pine plantations (32% of the area), *Araucaria* plantations (4%), and native forest (64%), and had contiguous or overlapping home ranges (yearly home-range percent overlap of each group with groups of the other species: 41–99%; overlap with group of the same species: 0–38% [Agostini et al. 2010b]). Native forest, the habitat type containing most of the food plant species of the howler monkeys, represented 65.11% of the home range for BR1, 34.22% for BR2, 63.55% for BL1, and 59.94% for BL2 (Agostini et al. 2010b). All 4 groups were previously habituated, and most group members were identified individually by natural markings.

Data collection.—During the 12-month study period, IA and IH, with the help of 1 or 2 field assistants at a time, spent 3.02 days (± 0.60 *SD*; range 1–5 days) per month following each howler group (for BR1 group, the October sample, for which we had only a 1-day follow, was not considered in data analysis). We collected data on group activity by scan sampling (Altmann 1974) at 10-min intervals, totaling 1,846 scans over 308 h of observation for group BR1, 2,113 scans over 352 h for BR2, 2,103 scans over 351 h for BL1, and 2,298 scans over 383 h for BL2. Except for a few gaps, when groups were out of view, scan sampling was continuous throughout the day, and its time span varied according to day length, beginning as early as 0550 and finishing as late as 1930 h.

We always took a group scan if ≥1 individual came into view during the scan period. Whenever possible we recorded the identity of the scanned subjects, otherwise, we assigned the individual to 1 of 5 age–sex classes following the classifications of Mendes (1989) and Rumiz (1990): adult males, adult females, subadult males, subadult females, or juveniles of either sex. We watched the individual for 5 s after it came into view and recorded the predominant activity (Clutton-Brock 1977b). We referred to the observations of each scanned individual as a ''behavioral record.'' We tried to collect behavioral records on as many individuals as possible during a scan ($\bar{X} \pm SD$ number of individuals/scan: 5.77 ± 1.78 for BR1, 3.69 ± 0.64 for BR2, 6.80 ± 2.57 for BL1, 4.93 ± 1.50 for BL2).

The following 5 mutually exclusive activity categories were recorded for each individual during a scan: resting (inactive, in either a sitting, lying, standing, or suspended posture; including the infrequent autogrooming activity); moving (changing spatial position, only including short, nondirectional movements in cases in which the group is engaged in nontraveling activities); traveling (changing location directionally, in a context of group traveling in a goal-oriented direction); feeding (procuring, handling, ingesting, or chewing any food item; it includes the infrequent drinking activity); social (engaging in any behavior involving the interaction with 1 or more other individuals, such as allogrooming, playing, mating, and agonistic interactions); and other (engaging in infrequent behaviors, such as vocalizing, defecation–urination, scent-marking, etc., that do not otherwise fall into any of the previously defined categories).

To estimate food availability, we combined monthly phenological data (2 trails; 6.65 km total length; 253 trees of 40 different plant food species with diameter at breast height $\geq$ 10 cm) with vegetation survey data (209 points along transects sampled with the point-quarter method—Krebs 1989) of the 3 main habitat types (pine plantations, *Araucaria* plantations, and native forest) within the home ranges of the study groups. For each species and phenophase, in each habitat type, we obtained a monthly food availability index by multiplying the phenological index for the species by the basal area (m^2/ha) estimated in the vegetation survey. We then calculated a food availability index for each plant species as the average of the 3 habitat-specific food availability indexes, weighted by the proportion of representation of each habitat type in the entire study area. Finally, we calculated a monthly total food availability index for each phenophase by adding food availability indexes across all plant food species. More details about the methods used for estimating food availability, as well as methods used to analyze the groups' dietary profiles, are reported in related articles (Agostini et al. 2010a, 2010b). We followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) in all of our research procedures.

Data analyses.—We calculated time budgets for each howler group following Clutton-Brock (1977b). First, we calculated the time allocated to each activity for each scan as the proportion of scanned individuals engaged in each activity. Then, to reduce the potential biases introduced by differences in the number of scans collected in different months or at different times of the day, we 1st calculated hourly time budgets by averaging scan budgets for each hour, then monthly budgets by averaging hourly budgets for each month, and yearly budgets by averaging monthly budgets.

The daily activity pattern (i.e., the diurnal distribution of activities) of each howler group was expressed as the average proportion of time spent in each of the major activities (rest, move + travel, and feed) in hourly classes from 0600 to 1900 h (the class 0600 h represented data from 0600 to 0700 h, and so on throughout the day).

Finally, the activity budget of each age–sex class was expressed as the number of behavioral records engaged in each activity divided by the total number of behavioral records. Given that traveling was a rather synchronized activity among members within a group, for age–sex class analysis, we considered only moving, which is likely to vary more among the age–sex classes of a group. We excluded the subadult female category in the age–sex analyses, because it was represented only by 1 individual in 1 group (BL2) during 4 months.

The study period was divided into 12 monthly samples for the 4 groups, except BR1, which lacked the October sample. Each sample was obtained within 10 days of the 2-day periods of plant phenology monitoring (see Agostini et al. 2010a), so that behavioral observations can be tightly correlated with monthly estimates of food availability. Comparisons of time budgets between groups or species were performed on a monthly basis and on a seasonal basis. For the latter type of analysis, we considered 2 seasons according to the changes in highest-quality food availability and temperature: a 4-month lean season (May–August) that corresponded to the coldest season and to the time of the year with the highest consumption of mature leaves by howlers, and an 8-month abundant season (September–April) that corresponded to the warmest season and to the period of highest relative consumption of fleshy fruits and young leaves (Agostini et al. 2010a). Day length (from sunrise to sunset) in the region varies between 13 h 46 min in December and 10 h 30 min in June. This difference in time availability means that animals have different total amounts of time available to accommodate their activity budgets across seasons. To control for this, in the analyses of seasonal variation, we used the monthly total amount of daylight time spent in each activity, calculated by multiplying the proportion of each hourly sample devoted to each activity during a particular month by 60 min, and summing the minutes across all daylight hours.

We used parametric tests whenever residuals of data were normally distributed; otherwise, we used nonparametric statistics (Sokal and Rohlf 1995). To test for the influence of seasonality on activity patterns, we analyzed seasonal differences in the amount of daylight time spent in each activity within each species by using a 2-way analysis of variance (ANOVA), controlling for group identity and interaction between season and group identity. Further, to evaluate the effect of potential predictor variables on monthly activity budgets within each howler species, we generated a stepwise multivariate analysis of covariance (ANCOVA) model with group identity, availability and proportions of young leaves, mature leaves, fruits, and flowers in the diet, rainfall, and average maximum and minimum temperatures as the independent variables. To analyze the relationship between activity budget and temperature, which is predicted to be

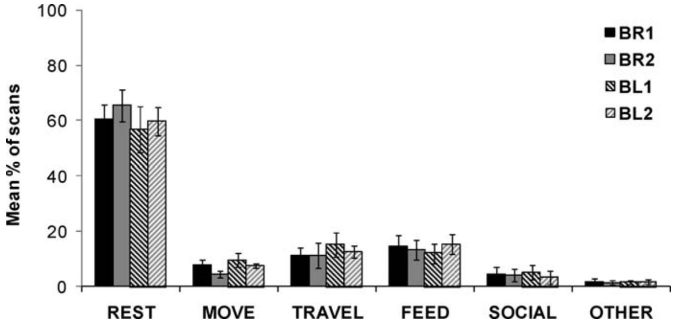

FIG. 2.—Mean (± *SD*) percent yearly budgets of activities for the 4 study groups (BR1, BR2, BL1, and BL2).

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.

To evaluate the influence of group size on time budgets, we used a 2-way ANOVA to test for the effect of group identity and month on monthly proportions of each activity within each howler species. Then, we used linear regressions to assess the relationship between group size and annual activity budgets and ANCOVAs to test the effects of the covariate group size and the independent variable, season, on the amount of daylight time devoted to each activity, across both howler species. Differences in activity budgets between age–sex classes within each species across months were analyzed using a 2-way Friedman ANOVA and a Wilcoxon matched-pairs test for subsequent comparisons between pairs of age–sex classes.

Finally, to evaluate the effect of presence of a congener on howler time allocation patterns, between-species comparisons of monthly time budgets were made using a 2-way ANOVA testing for the effect of species and month on monthly proportions of time devoted to each activity. Subsequently, we performed a 2-way ANOVA to test for seasonal differences in the amount of daylight time devoted to each activity between species. Moreover, we described the daily distribution of feeding activity patterns of groups of different species using circular statistics. For each group and season, we calculated the concentration parameter: a mean vector with magnitude r, indicating the relative dispersion of the observations (range value 0–1; if the activity is concentrated in a 1-h interval r will approximate 1; if the activity is randomly distributed, then r will be near 0), and an orientation, Θ, representing the location (angle) on a 24-h cycle of the mean vector direction (Fisher 1993).

We used 1-tailed statistical tests whenever predictions from our hypotheses were clearly directional (i.e., for the variables moving, traveling, and resting), and indicated the relative *P*-values as ''$P_{1\text{-tail}}$'' in the results, otherwise we used 2-tailed tests, with α set at 0.05. All tests were performed with Statistica 5.5 (Statsoft Inc., Tulsa, Oklahoma) and JMP 3.2.6 (SAS Institute Inc., Cary, North Carolina) statistical software.

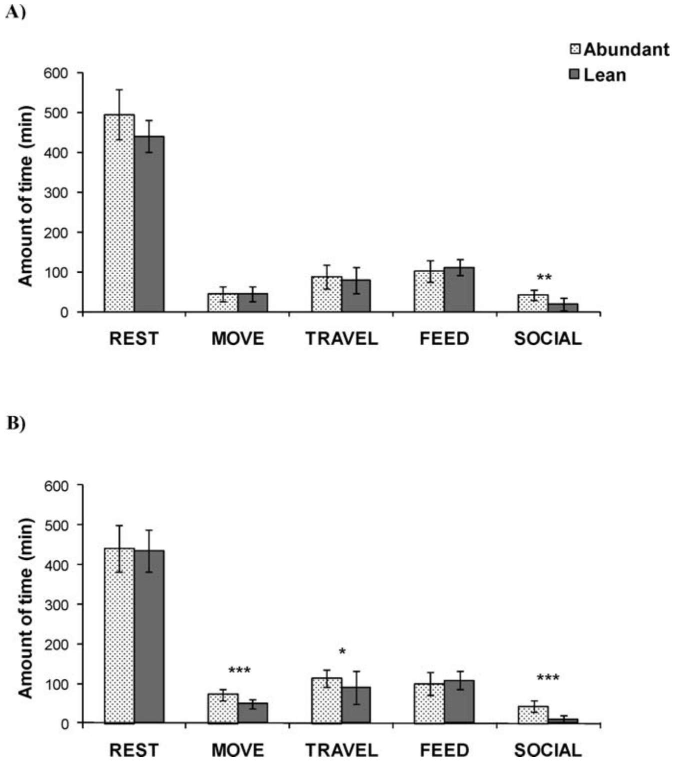

FIG. 3.—Seasonal differences in the mean amount of daylight time (expressed as minutes) spent in each activity for A) brown howlers and B) black-and-gold howlers. Bars represent standard deviations. Abundant season (September–April); lean season (May–August). Asterisks indicate levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

RESULTS

Overall, all 4 study groups spent the greatest proportion of daytime (57–65%) resting. Moving and traveling accounted on average for 4–10% and 11–15%, respectively, and feeding for 12–15% of monthly time budgets. All groups devoted a small proportion of time on average to social (3–5%) and other (1–2%) activities (Fig. 2).

Effect of seasonality.—Regardless of group identity, brown howlers allocated a significantly greater amount of time to social behavior in the abundant season compared to the lean season (season: $F_{1,19} = 12.98$, $P = 0.002$; group identity: $F_{1,19} = 0.06$, $P = 0.800$; Fig. 3A). Black-and-gold howlers spent a significantly greater amount of time moving ($F_{1,20} = 31.41$, $P_{1\text{-tail}} < 0.001$), traveling ($F_{1,20} = 3.47$, $P_{1\text{-tail}} = 0.039$), and social ($F_{1,20} = 39.07$, $P < 0.001$) in the abundant season compared to the lean season (Fig. 3B). Individuals of the largest BL1 group spent a greater amount of time moving ($F_{1,20} = 7.30$, $P_{1\text{-tail}} = 0.007$), traveling ($F_{1,20} = 3.49$, $P_{1\text{-tail}} = 0.038$) and social ($F_{1,20} = 5.34$, $P = 0.032$), but a smaller amount of time feeding ($F_{1,\ 20} = 4.82$, $P = 0.040$), than individuals of the smallest BL2 group. Also, the greater time spent moving in the abundant season compared to the lean season depended on group identity, being evident in the largest group, but not in the smallest one (group identity × season: $F_{1,20} = 9.81$, $P = 0.005$). For both species, the amount of time dedicated to all other activities did not vary significantly between seasons (all $P \geq 0.411$), and group and season effects never interacted significantly in other comparisons (all $P \geq 0.117$).

Results of the stepwise multivariate ANCOVA model show that, for brown howlers, the proportion of time spent resting was significantly smaller for individuals in the largest group than for individuals in the smallest group ($F_{1,1} = 6.80$, $P_{1\text{-tail}} = 0.009$), and showed a negative relationship with ripe fruit availability ($F_{1,1} = 3.59$, $P_{1\text{-tail}} = 0.036$; $R^2_{\text{adj}} = 0.24$); the proportion of time spent moving was greater for individuals in the largest group than for individuals in the smallest group ($F_{1,1} = 28.44$, $P_{1\text{-tail}} < 0.001$), and increased with the proportion of flowers in the diet ($F_{1,1} = 4.97$, $P_{1\text{-tail}} = 0.019$; $R^2_{\text{adj}} = 0.58$); the proportion of time spent feeding decreased with mature leaves availability ($F_{1,1} = 8.69$, $P = 0.008$; $R^2_{\text{adj}} = 0.26$), and the proportion of time spent in social behaviors increased linearly with minimum temperature ($F_{1,1} = 14.17$, $P = 0.001$; $R^2_{\text{adj}} = 0.40$). Other variables did not show statistically significant effects.

For black-and-gold howlers, the proportion of time spent resting decreased with the availability of ripe fruits ($F_{1,1} = 4.95$, $P_{1\text{-tail}} = 0.019$) and increased with the proportion of mature leaves in the diet ($F_{1,1} = 5.99$, $P_{1\text{-tail}} = 0.012$; $R^2_{\text{adj}} = 0.28$); the proportion of time spent moving was significantly greater for individuals in the largest group than for individuals in the smallest group ($F_{1,1} = 4.38$, $P_{1\text{-tail}} = 0.024$), and increased with the proportion of young leaves in the diet ($F_{1,1} = 8.18$, $P_{1\text{-tail}} = 0.005$; $R^2_{\text{adj}} = 0.38$); the proportion of time devoted to traveling was significantly greater for individuals in the largest group than for individuals in the smallest group ($F_{1,1} = 5.43$, $P_{1\text{-tail}} = 0.015$), and increased with the proportion of ripe fruits in the diet ($F_{1,1} = 2.97$, $P_{1\text{-tail}} = 0.050$; $R^2_{\text{adj}} = 0.18$), also, the residuals of this model showed the predicted curvilinear relationship (2-degree polynomial) between traveling budget and maximum and minimum temperatures (maximum temperature: $F_{2,21} = 3.60$, $P_{1\text{-tail}} = 0.023$; minimum temperature: $F_{2,21} = 3.77$, $P_{1\text{-tail}} = 0.020$); the proportion of time devoted to feeding was significantly smaller for the largest group than for the smallest group ($F_{1,1} = 10.56$, $P = 0.004$) and decreased with mature leaves availability ($F_{1,1} = 25.35$, $P < 0.001$; $R^2_{\text{adj}} = 0.60$); the time spent in social behaviors was significantly greater for the largest group than for the smallest group ($F_{1,1} = 9.76$, $P = 0.005$), and showed a significant positive relationship with maximum temperature ($F_{1,1} = 10.71$, $P = 0.004$) and a nearly significant positive relationship with minimum temperature ($F_{1,1} = 4.31$, $P = 0.051$; $R^2_{\text{adj}} = 0.72$). All other variables showed no statistically significant effect.

Effect of group size and composition.—Within brown howlers, individuals in the largest group spent proportionately less time resting and more time moving, and tended to spend more time feeding than individuals in the smallest group across months (rest: $F_{1,10} = 5.16$, $P_{1\text{-tail}} = 0.023$; move: $F_{1,10} = 17.68$, $P_{1\text{-tail}} = 0.001$; feed: $F_{1,10} = 4.03$, $P = 0.073$), but traveling and social budgets were not significantly affected by group identity (all $P \geq 0.504$). Month effect was significant only for feeding ($F_{11,10} = 6.67$, $P = 0.003$). Within black-and-gold howlers, individuals in the largest group spent significantly higher proportions of time moving, traveling, and social, but lower proportions of time feeding than individuals in the smallest group across months (move: $F_{1,11} = 7.45$, $P_{1\text{-tail}} = 0.010$; travel: $F_{1,11} = 4.26$, $P_{1\text{-tail}} = 0.032$; feed: $F_{1,11} = 16.62$, $P = 0.002$; social: $F_{1,11} = 9.85$, $P = 0.009$). Resting budgets were not significantly affected by group identity ($F_{1,11} = 1.63$, $P_{1\text{-tail}} = 0.114$). Month effect was significant only for feeding ($F_{11,11} = 5.63$, $P = 0.004$) and social ($F_{11,11} = 5.58$, $P = 0.004$).

Considering together all 4 howler groups, we found a negative and nearly significant linear relationship between group size and annual resting budgets ($F_{1,1} = 8.40$, $P_{1\text{-tail}} = 0.051$; $R^2_{\text{adj}} = 0.71$; Fig. 4A), and positive and near-significant linear relationships between group size and annual moving budgets ($F_{1,1} = 9.84$, $P = 0.088$; $R^2_{\text{adj}} = 0.75$; Fig. 4B) and between group size and annual traveling budgets ($F_{1,1} = 6.80$, $P_{1\text{-tail}} = 0.060$; $R^2_{\text{adj}} = 0.66$; Fig. 4C), but no relationship between group size and feeding or social budgets ($P \geq 0.315$). Moreover, when taking into account the simultaneous effects of group size and seasons on the amount of time spent in each activity, we found that, as predicted, the amount of time spent traveling was greater for larger groups and during the abundant season (group size: $F_{1,1} = 11.85$, $P_{1\text{-tail}} = 0.009$; season: $F_{1,1} = 5.43$, $P_{1\text{-tail}} = 0.\ 034$; $R^2_{\text{adj}} = 0.68$), whereas the time spent moving tended to be greater for larger groups but not during the abundant season (group size: $F_{1,1} = 6.38$, $P = 0.053$; season: $F_{1,1} = 1.93$, $P_{1\text{-tail}} = 0.\ 112$; $R^2_{\text{adj}} = 0.47$). Similarly, the amount of time spent resting was smaller for larger groups but was not affected by season (group size: $F_{1,1} = 6.76$, $P_{1\text{-tail}} = 0.024$; season: $F_{1,1} = 4.30$, $P_{1\text{-tail}} = 0.954$; $R^2_{\text{adj}} = 0.56$). Finally, the amount of time spent in social behavior was greater during the abundant season but was not affected by group size (group size: $F_{1,1} = 0.60$, $P = 0.474$; season: $F_{1,1} = 23.65$, $P = 0.005$; $R^2_{\text{adj}} = 0.76$), whereas the time spent feeding was not affected by any of the 2 variables ($P \geq 0.171$).

Age–sex classes differed significantly in the proportions of time allocated to resting, moving, and social, but not to feeding, both in brown howlers (resting: $\chi^2_3 = 29.70$, $P < 0.001$; moving: $\chi^2_3 = 29.70$, $P < 0.001$; social: $\chi^2_3 = 13.70$, $P = 0.003$; feeding: $\chi^2_3 = 6.30$, $P = 0.098$) and black-and-gold howlers (resting: $\chi^2_3 = 26.20$, $P < 0.001$; moving: $\chi^2_3 = 25.80$, $P < 0.001$; social: $\chi^2_3 = 21.90$, $P < 0.001$; feeding: $\chi^2_3 = 6.50$, $P = 0.090$), across months. In particular, within brown howlers, although adult males and females spent proportionately more time resting, immatures (juveniles + subadult males) moved more, and juveniles socialized more than the other classes. Similarly, within black-and-gold howlers, juveniles spent proportionally less time resting and more time moving and social than adults and subadult males (Table 2).

Influence of presence of a congener.—Overall, brown howlers devoted proportionately more time to rest ($F_{1,34} = 7.26$,

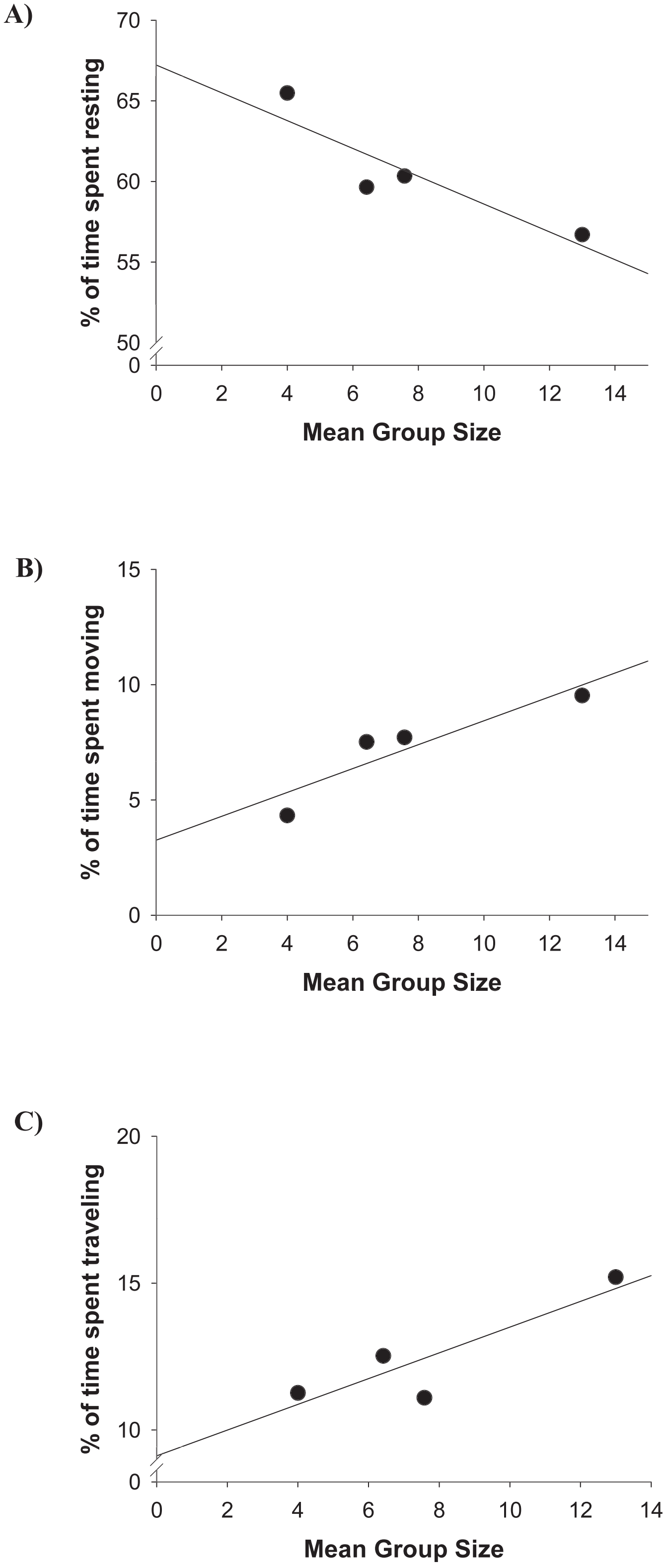

FIG. 4.—Linear regression between mean group size and percent of time spent A) resting, B) moving, and C) traveling, for both howler species.

$P = 0.011$) and less time to moving ($F_{1,34} = 13.76$, $P < 0.001$) and traveling ($F_{1,34} = 8.11$, $P = 0.007$) than black-and-gold howlers across months. No difference was found in the proportion of time devoted to feeding ($F_{1,34} = 0.17$, $P = 0.680$) or social behavior ($F_{1,34} = 0.25$, $P = 0.618$) between species. The month effect was significant for traveling ($F_{11,34} = 2.71$, $P = 0.013$), feeding ($F_{11,34} = 3.22$, $P = 0.004$), and social ($F_{11,34} = 5.58$, $P < 0.001$). During periods of food scarcity both howler species devoted a smaller amount of time to moving ($F_{1,43} = 5.03$, $P_{1\text{-tail}} = 0.015$) and social behavior ($F_{1,43} = 39.27$, $P < 0.001$), but did not change the amount of time spent resting ($F_{1,43} = 2.99$, $P_{1\text{-tail}} = 0.955$) or feeding ($F_{1,43} = 1.24$, $P = 0.271$; Figs. 3A and 3B). In addition, black-and-gold howlers spent a greater amount of time moving ($F_{1,43} = 9.60$, $P = 0.003$) and tended to spend more time traveling ($F_{1,43} = 4.01$, $P = 0.052$) than brown howlers, but the species did not differ in the amount of time spent in other activities (all $P \geq 0.091$). There was only 1 statistically significant interaction between species and seasons: the decrease of moving time from the abundant to the lean season was more pronounced for black-and-gold howlers than for brown howlers ($F_{1,43} = 5.36$, $P = 0.026$).

As a direct consequence of the difference in daylight time available, the hours during which howlers were active shifted between seasons. In the lean season, activities began about 1 h later and finished about 1 h earlier compared to the abundant season. All groups rested more during midday–early afternoon hours during the hottest abundant season, whereas they remained inactive for most of the morning hours during the coldest lean season (Fig. 5). During both seasons, all howler groups had similar general peaks of activity during the day, except for feeding, that presented more pronounced and distinct peaks for each group in the lean season. The higher concentration of daily feeding (at least for 3 of the 4 study groups: BR2, BL1, and BL2) and the greater divergence of feeding peaks among groups in the lean season compared to the abundant season also is evident when looking at the location of the concentration parameters (Figs. 6A and 6B). However, contrary to our prediction, there was not a clear pattern of more divergent peaks for the most range-overlapping groups (BR1–BL2 and BR2–BL1) compared with the least (or non-) range-overlapping groups (BR1–BR2, BL1–BL2; BR1–BL1; and BR2–BL2; Figs. 5, 6A, and 6B).

DISCUSSION

Brown howlers and black-and-gold howlers presented some differences in the seasonal patterns of activity at our site. Specifically, although for brown howlers our results provided limited support for only 2 of the 3 predictions of the hypothesis of energy minimization (less time resting with increasing ripe fruit availability, and more time moving with increasing flower consumption), for black-and-gold howlers, we found extensive support for all 3 predictions of this hypothesis (less time resting with increasing ripe fruit availability and more time resting with increasing mature leaf consumption; more time moving with increasing young leaf consumption; and more time traveling with increasing ripe fruits in the diet, and at intermediate temperatures but decreasing at extreme temperature values). Studies on both

TABLE 2.—Wilcoxon matched-pairs test: *t*- and *P*-values for comparisons of monthly percentages of time budgets between age–sex classes (ADM = adult males; ADF = adult females; SBM = subadult males; JUV = juveniles) of brown howlers (left) and black-and-gold howlers (right). Significant differences after applying Bonferroni correction for multiple tests ($\alpha' = 0.008$) are in boldface italic type.

		Brown howlers			Black-and-gold howlers		
Activity	Age–sex pairs	*t*	*P*		*t*	*P*	
Rest	ADM versus ADF	8	0.015		**3**	**0.005**	(ADM > ADF)
	ADM versus SBM	**0**	**0.002**	(ADM > SBM)	**3**	**0.005**	(ADM >SBM)
	ADM versus JUV	**0**	**0.002**	(ADM > JUV)	**0**	**0.002**	(ADM> JUV)
	ADF versus SBM	**1**	**0.003**	(ADF > SBM)	21	0.158	
	ADF versus JUV	**0**	**0.002**	(ADF > JUV)	**1**	**0.003**	(ADF > JUV)
	SBM versus JUV	36	0.814		**0**	**0.002**	(SBM > JUV)
Move	ADM versus ADF	**1**	**0.003**	(ADM < ADF)	**2**	**0.004**	(ADM < ADF)
	ADM versus SBM	**0**	**0.002**	(ADM < SBM)	**5**	**0.008**	(ADM < SBM)
	ADM versus JUV	**0**	**0.002**	(ADM < JUV)	**0**	**0.002**	(ADM < JUV)
	ADF versus SBM	**0**	**0.002**	(ADF < SBM)	37	0.875	
	ADF versus JUV	**1**	**0.003**	(ADF < JUV)	**0**	**0.002**	(ADF < JUV)
	SBM versus JUV	23	0.209		**2**	**0.004**	(SBM < JUV)
Feed	ADM versus ADF	25	0.272		17	0.084	
	ADM versus SBM	16	0.071		22	0.182	
	ADM versus JUV	17	0.084		9	0.019	
	ADF versus SBM	16	0.071		32	0.583	
	ADF versus JUV	29	0.433		11	0.028	
	SBM versus JUV	26	0.308		20	0.136	
Social	ADM versus ADF	32	0.583		32	0.583	
	ADM versus SBM	22	0.182		16	0.071	
	ADM versus JUV	**4**	**0.006**	(ADM < JUV)	**1**	**0.003**	(ADM < JUV)
	ADF versus SBM	23	0.209		10	0.023	
	ADF versus JUV	**3**	**0.005**	(ADF < JUV)	**0**	**0.002**	(ADF < JUV)
	SBM versus JUV	**3**	**0.005**	(SBM < JUV)	**0**	**0.002**	(SBM < JUV)

howler species at other sites have explained variations in activity patterns on the basis of availability or consumption of particular foods (Chiarello 1993; Mendes 1989), or on the basis of climatic factors such as temperature (Chiarello 1993), or both. Although we cannot discard that our study groups may have differed slightly in food availability, the high home-range overlap between groups of different species at El Piñalito (Agostini et al. 2010b) suggests that this may be not the most likely explanation for the between-species difference found. Assuming environmental and climatic conditions were equal for both howler species at our study site, other possible explanations, such as between-species differences in physiological state or in specific food items consumed in certain periods by one species but not the other, may account for the difference found. Moreover, the discrepancy between the responses of the 2 howler species to food seasonality also is reflected in their ranging behavior: although black-and-gold howlers significantly increased their daily ranges in the abundant season and in response to the increased percentage of fruits in diet, the brown howlers' ranging patterns did not change between seasons or according to food availability and consumption (Agostini et al. 2010b).

Although we found seasonal variation for most activities, the absolute amount of time spent feeding did not significantly differ between seasons, suggesting that howlers cannot simply increase the feeding time according to the increasing amount of daylight hours available during the abundant season. No matter how much ripe fruit is available in their habitat, howlers invariably eat some leaves each day (Chapman 1988; Glander 1978; Milton 1980). The limited adaptations to folivory of howler monkeys include enlarged surface areas in the colon or caecum, or both, and a long retention time of food in the gastrointestinal tract, allowing more time for fermentation and nutrient absorption (Lambert 1998; Milton 1998). Therefore, their typical slow digestion rates could represent a physiological constraint on the amount of time spent feeding in the abundant season.

Some of the variation in time budgets observed in both howler species at El Piñalito can be explained by differences in group size and composition. For both species, the greater proportions of moving or traveling time, or both, spent by individuals in larger groups compared to individuals in smaller groups and, only for brown howlers, the smaller proportion of resting time and the greater proportion of time spent feeding by individuals in larger groups compared to individuals in smaller groups widely support the hypothesis that the degree of within-group competition for food increases with group size (Chapman and Chapman 2000; Janson and Goldsmith 1995). This finding is in agreement with other lines of evidence provided by Snaith and Chapman (2007), suggesting that folivorous primate species, and not only frugivorous ones, experience within-group scramble-feeding competition and their group size may be ecologically constrained. In particular, given that folivorous or partially folivorous species, such as howler monkeys, are often highly selective feeders relying on patchily distributed food sources (e.g., young leaves [Chapman et al. 2003; Milton 1980]), they may actually deplete food patches (Leighton and Leighton 1982), and are likely to be

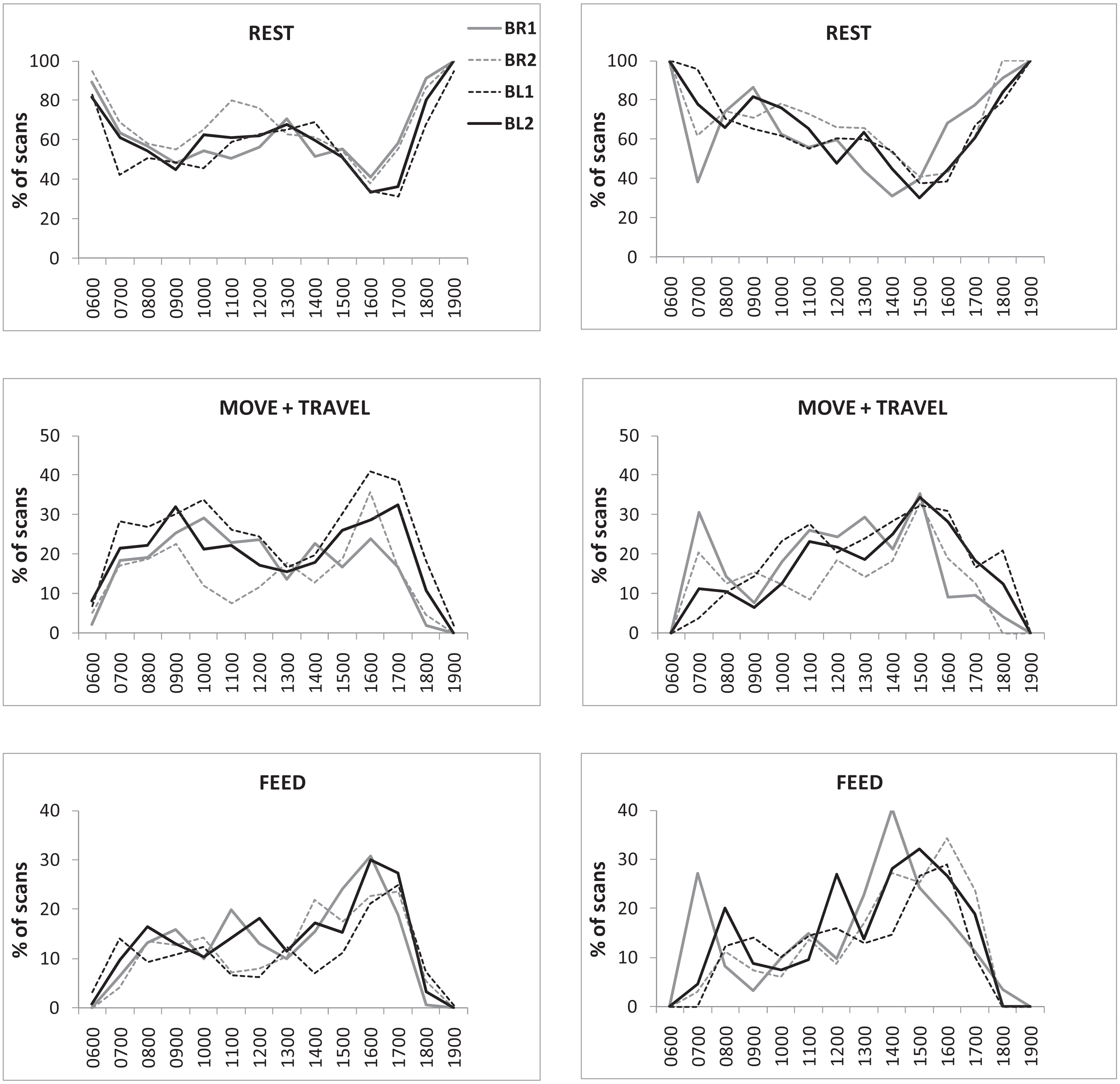

Fig. 5.—Daily distribution of resting, moving + traveling, and feeding, from 0600 to 1900 h, during the abundant season (left column) and the lean season (right column), for brown howler (BR) groups (gray) and black-and-gold howler (BL) groups (black). Groups with the greatest home-range overlap are represented by similar line features (BR1 and BL2: continuous lines; BL1 and BR2: dotted lines).

subject to similar ecological constraints as frugivores, and may respond with similar competitive regimes (but see Janson and Goldsmith 1995). Although our results support the hypothesis of within-group feeding competition, we cannot rule out an alternative explanation for group differences in activity patterns, such as differences in food-patch distribution among different-sized groups (e.g., larger groups may travel more due to larger distances between food patches within their home ranges). However, given the great home-range overlap between large and small groups of different species (BR1 and BL2, and BL1 and BR2—Agostini et al. 2010b), we think it is unlikely that different patch distributions play an important role in determining differences in time spent traveling between larger and smaller groups. Further, the qualitative homogeneity of habitat in the study area (i.e., the pine plantations had exactly the same age, and the native forest used by the different groups was qualitatively similar in structure and composition and had a common history of timber exploitation) renders it unlikely that there are important differences in mean food-patch size and distribution among

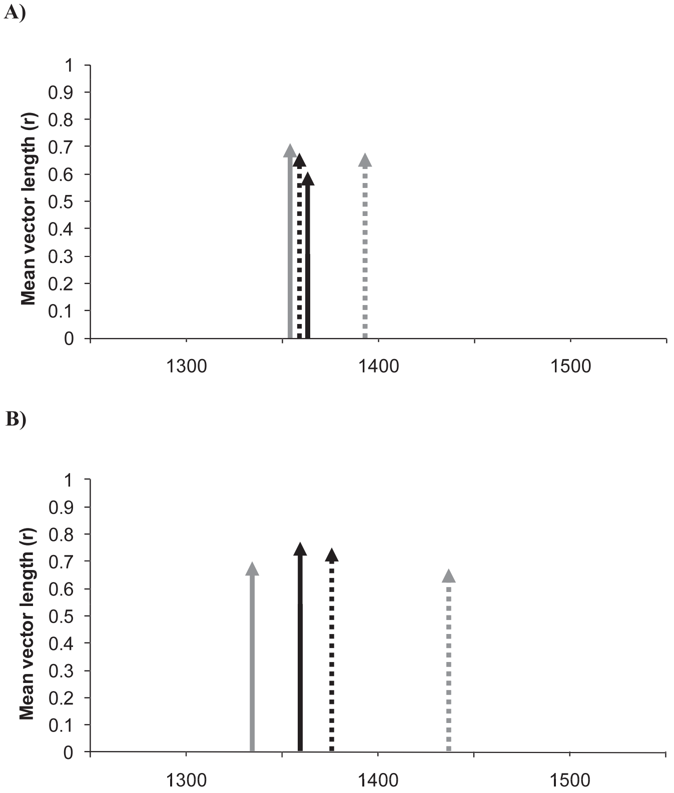

FIG. 6.—Concentration parameter of daily feeding patterns A) in the abundant season and B) in the lean season for brown howler (BR) groups (gray) and black-and-gold howler (BL) groups (black). Arrows are positioned at the time of the day in which feeding is more concentrated. The arrow lengths represent the degree of concentration of daily feeding. Groups with the greatest home-range overlap are represented by similar line features (BR1 and BL2: continuous arrows; BL1 and BR2: broken arrows).

home ranges of different groups. Nevertheless, future studies should include measures of food-patch distribution for each group as another source of potential variation in activity patterns among groups.

Group composition was a further important factor influencing time budgets of both species. On one hand, the higher levels of locomotor and social activities we found in juveniles compared to adults match results of other studies on howler monkeys (Bicca-Marques and Calegaro-Marques 1994; Prates and Bicca-Marques 2008) and primates in general (Pereira and Fairbanks 1993), and could be the result of a general adaptation for the development of foraging and social skills in mammals (Martin and Caro 1985). On the other hand, juveniles of both species, despite their smaller size and consequent lower absolute metabolic needs (Kleiber 1961; McNab 1980), spent a comparable percent of time feeding relative to adults. This result could be explained by the fact that juvenile primates are generally less efficient foragers than adults, and may compensate this disadvantage by increasing their foraging effort in order to fulfill their energetic requirements (Janson and van Schaik 1993).

A few differences in time budgets also were found between the 2 howler species. Black-and-gold howlers rested less and moved and traveled more than syntopic brown howlers, but this could be due to the larger sizes of their groups. However, the relatively limited number of groups available for this study does not allow us to distinguish to what extent this time-budget difference is better explained by group size or by species-specific traits. However, the former seems to be a more parsimonious explanation given the strong similarity in diet and behavior between the species at the study site (Agostini 2009; Agostini et al. 2010a).

Groups of different howler species showed just slight differences in peak times of feeding in the lean season. By changing how they distribute crucial activities, such as feeding throughout the day, sympatric species can reduce their degree of interspecific contest competition during periods of food shortage (Schoener 1974; Tokeshi 1999). However, time partitioning may be phylogenetically constrained (Roll et al. 2006) and, as a result, has been proposed mainly for mammalian taxa that are cathemeral or for which the transition from a diurnal to a nocturnal lifestyle has been evolutionarily feasible (Di Bitetti et al. 2009, 2010; Overdorff 1996; Paviolo et al. 2009; Sussman 1974; Wright 1989). In these groups, species may be able to flexibly adjust their activity pattern to local conditions of competition or predation, or both. In contrast, strictly diurnal taxa, such as howlers, or strictly nocturnal ones, such as bats (which face significant time constraints to their activity, especially at high latitudes due to seasonal changes in day length), may have very restricted opportunities for temporal partitioning (but see Rydell 1993; Singh et al. 2000). At El Piñalito, brown howler and black-and-gold howler groups showed high dietary overlap throughout the year (Agostini et al. 2010a), and overlapped greatly in their ranging areas during periods of food scarcity (Agostini et al. 2010b). The subtle partitioning of daily feeding time may smooth the high potential competition in times of food shortage. Nevertheless, because we did not find a clear pattern of peak differentiation between the most range-overlapping groups compared to the least (or non-) range-overlapping groups, we must rule out the hypothesis that this time partitioning represents a response to local competition between species.

Finally, examination of the data on feeding activity showed 3 daily peaks of feeding activity for all groups, separated by 3–4 h (Fig. 5). Likely, the fact that this pattern was more pronounced in the lean season than in the abundant season (Fig. 5) may have to do with the fact that both species ingested more mature leaves in the lean season (Agostini et al. 2010a). Mature leaves are a relatively abundant but difficult to digest material compared to other items of the diet (Lambert 1998). Examination of our data suggests that it takes 3–4 h for a full stomach to empty to the point that a howler is willing to exert the effort to find and ingest additional food. The time required to empty the stomach results in these distinct 3 peaks of feeding activity and may further restrict the options available to switch their daily feeding patterns to reduce competition during the lean season.

In conclusion, we suggest that at El Piñalito, although brown howler and black-and-gold howler groups showed some differences in time allocation patterns (mainly related to differences in their response to food seasonality, and in group size) there is no evidence of partitioning in the use of time for a crucial activity such as feeding. The great overlap in temporal niche, together with the great overlap in trophic and spatial niches (Agostini et al. 2010a, 2010b), suggests that niche differentiation is not occurring along any of the gross ecological axes between these 2 syntopic species. Mammalian taxa, such as howlers, that have entrenched adaptations (i.e., a phylogenetic constraint) for a strictly diurnal lifestyle have low opportunities for using time partitioning as a mechanism to reduce interspecific competition among closely related species. As a result, the great ecological overlap and the potential for interspecific competition among ecologically similar and closely related species of *Alouatta* could be the mechanisms responsible for their essentially parapatric distributions.

Resumen

Especies ecológicamente similares y filogenéticamente cercanas pueden diferenciarse en sus patrones de actividad cuando viven en simpatría para evitar la competencia directa. Presentamos el primer estudio que tuvo el objetivo de evaluar los efectos de la estacionalidad, el tamaño de grupo y la presencia de una especie congenérica sobre los patrones de actividad de 2 especies sintópicas de monos aulladores, el aullador marrón (*Alouatta guariba clamitans*) y el aullador negro y dorado (*A. caraya*), en el noreste de Argentina. Durante 12 meses colectamos datos de actividad de 2 grupos de cada especie de aullador junto con datos de disponibilidad de alimentos. Analizamos la variación estacional en la cantidad de tiempo dedicada a cada actividad y en los patrones diarios de actividad, así como las relaciones entre los presupuestos mensuales de actividad y la disponibilidad de alimentos, la dieta y el clima, tanto dentro de cada especie como entre especies diferentes. Los aulladores negros y dorados adoptaron más claramente que los aulladores marrones una estrategia de minimización de energía, reduciendo las actividades más costosas, como movimiento y desplazamiento, durante la estación de escasez de alimento. Dentro de cada especie, los individuos en el grupo más grande mostraron una mayor proporción de tiempo en movimiento o desplazamiento que los individuos en el grupo más pequeño, lo cual sugiere la existencia de competencia intra-grupal por el alimento. Los juveniles de ambas especies dedicaron proporcionalmente menos tiempo al descanso y más tiempo al movimiento y a la socialización que los adultos. Los aulladores negros y dorados dedicaron proporcionalmente más tiempo al movimiento y menos tiempo al descanso que los aulladores marrones, probablemente debido al mayor tamaño medio de los grupos de la primera especie. Los picos diarios de alimentación solo divergieron ligeramente entre grupos en la época de escasez de alimento, pero las diferencias entre grupos de especies diferentes cuyas áreas de acción se solapan espacialmente no fueron mayores que las diferencias observadas entre grupos con solapamiento escaso o nulo (de la misma o de la otra especie). Nuestros resultados sugieren que aunque las 2 especies de aulladores muestran algunas diferencias en los patrones de actividad diaria, principalmente relacionadas a diferencias en sus respuestas a la estacionalidad de los recursos alimenticios y en el tamaño del grupo, no encontramos evidencia de partición de su nicho temporal.

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