American Journal of Primatology 78:825–837 (2016)

RESEARCH ARTICLE

Determinants of Daily Path Length in Black and Gold Howler Monkeys (*Alouatta caraya*) in Northeastern Argentina

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Models used to explain the social organization of primates suggest that variation in daily path length (DPL) is a response to variation in resource distribution and the intensity of intragroup feeding competition. However, daily path length may be affected by a number of other factors including the availability and distribution of nutritionally complementary food items, temperature which can influence activity budget, patterns of subgrouping, and the frequency and function of intergroup encounters. In this 6-month study (total 495 hr of quantitative data), we examined daily path lengths in two neighboring groups of black and gold howler monkeys (*Alouatta caraya*) inhabiting a semi-deciduous gallery forest in San Cayetano (27° 30′S, 58° 41′W), in the northwest province of Corrientes, Argentina. Both study groups were of similar size and composition. We identified relationships across groups between time spent feeding on fruits, leaves, and flowers, the number of trees visited, group spread, frequency of intergroup encounters, mean daily temperature, and DPL. Our results suggest that variation in food availability had a significant impact on howler ranging behavior by increasing DPL under conditions of high immature and mature fruit availability, and by decreasing DPL with increased availability and increased time invested in feeding on mature leaves. These results do not support the contention that a reduction in food availability or an increase in within-group feeding competition increased DPL in black and gold howler monkeys. DPL in black and gold howlers is influenced by several interrelated factors. In this regard we suggest that models of socio-ecology and ecological constraints need to reconsider how factors such as individual nutritional requirements, social tolerance and group cohesion, and the spatial and temporal availability of preferred and nearby food resources influence primate ranging behavior. Am. J. Primatol. 78:825–837, 2016. © 2016 Wiley Periodicals, Inc.

Key words: *Alouatta caraya*; black and gold howler monkey; daily path lengths; use of space; Argentina

INTRODUCTION

Daily path length (DPL), or the linear distance traveled during a single day, is commonly used as a measure of a primate's use of space, and the costs in time and energy of defending a territory and obtaining access to resources [Arrowood et al., 2003; Chapman & Chapman, 2000; Chapman et al., 1995; Clutton-Brock & Janson, 2012; Majolo et al., 2008; Milton, 1980; Pollard & Blumstein, 2008; Strier, 2000]. In this regard, models of primate socioecology predict that, in response to increased feeding competition associated with an increase in group size and/or a decrease in food availability, groups and their constituent members should often travel greater distances per day to encounter sufficient resources. As further or alternative ways of mitigating the costs of intragroup feeding competition, animals may also increase group spread or break into smaller subgroups that travel and forage independently [Chapman & Chapman, 2000;

Contract grant sponsor: The Cleveland Zoological Society; contract grant sponsor: Cleveland Metroparks Zoo; contract grant sponsor: PIP IU 355/CONICET-Argentina

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Received 4 May 2015; revised 9 March 2016; revision accepted 12 March 2016

DOI: 10.1002/ajp.22548

Clutton-Brock & Harvey, 1977; Clutton-Brock & Janson, 2012; Gillespie & Chapman, 2001; Isbell, 1991; Janson & Goldsmith, 1995; Snaith & Chapman, 2008].

However, there exists a growing body of evidence in several primate species, that group size is not a strong predictor of DPL [Arrowood et al., 2003; Chhangani & Mohnot, 2006; Chapman & Valenta, 2015; Fan et al., 2014; Gillespie & Chapman, 2001; Isbell, 1991; Sussman & Garber, 2011; Struhsaker & Leland, 1987], and that other factors such as dietary selectivity, intergroup interactions in response to mate and resource defense, predation and infanticide risk, and extra-group mating opportunities play a more prominent role in determining ranging patterns and DPL [Cowlishaw, 1997; Peres, 2000; Willems & Hill, 2009]. For example, in the case of western lowland gorillas (*Gorilla gorilla gorilla*), Doran-Sheehy et al. [2004] reported that DPL was positively correlated with the availability of fruits in the group's home range (fruit productivity explained 36% of variation in DPL in a multiple regression analysis). In a related study of the same species, Cipolletta [2004] found that the average monthly DPL was positively correlated with the percentage of fruit in gorilla fecal samples ($rs = 0.71$, $P < 0.05$) (during this period DPL wet season—fruits: 1,595 m, $n = 177$, $SD = 642$; dry season—no fruits: 1,326 m, $n = 149$, $SD = 432$). Similarly, using a multiple regression model to predict ranging patterns, Stevenson [2006] identified a positive relationship between DPL and both group size and fruit production in woolly monkeys (*Lagothrix lagothricha*). However, in a different population of woolly monkeys, Di Fiore [2003] found a nonsignificant relationship between (ripe) fruit production and DPL (i.e., DPL was not predicted by ripe fruit production, although in that study, ripe fruit consumption was predicted by ripe fruit availability). In contrast, DPL decreased with increased time spent fruit feeding in crested black macaques (*Macaca nigra*) [O'Brien & Kinnaird, 1997], and in the case of Eastern black and white colobus monkeys (*Colobus guereza*), Fashing [2001] reported that DPL was neither correlated with group size nor with time spent feeding on any particular food type.

Howler monkeys offer an instructive model for studying the relationships between daily path length, diet, changes in food availability, group cohesion, changes in food availability, and socioecology in nonhuman primates. Howlers are found to exploit a range of forest types including highly seasonal habitats and those severely modified by anthropogenic disturbance, and consume a diet principally composed of fruits, leaves, and flowers [Garber et al., 2015]. In addition, average group size within a species tends to vary minimally (6–18 except for *Alouatta palliata*). Groups generally contain only 2–4 adult females and 2–4 adult males and therefore the potential effects of group size on feeding ecology are minimized [Di Fiore et al., 2011]. In all howler species intergroup encounters associated with howling bouts and collective action involving several males and in some cases females are common, and are reported to influence ranging patterns, group movement, and within-group social bonds [Garber & Kowalewksi, 2011; Kitchen, 2004; Kowalewski & Garber, 2010, 2015; van Schaik & Janson, 2000].

Knopff & Pavelka [2006] studied the relationship between group size and two proxies of feeding competition—DPL and activity budget in three groups of black howler monkeys (*Alouatta pigra*) in Belize. After controlling for food availability, home range area, and group size, they found no significant differences in DPL or time spent feeding, foraging, traveling, or resting. Similarly, in a study of four groups of black howlers at another site in Belize, Arrowood et al. [2003] reported that group size had no effect on DPL, and that the strongest predictors of increasing DPL were increased group dispersion and increased time spent feeding on leaves. In contrast, in an 8 month study of two similar sized groups of *Alouatta caraya* on islands of continuously flooded forests in Northern Argentina, Bravo & Sallenave [2003] found that DPL was positively related to the frequency of intergroup encounters although the number of encounters was low during their 8 month study ($n = 14$ encounters). In this later study, however, the degree to which changes in food availability or female reproductive condition affected the frequency or location of intergroup encounters was not evaluated [Brown, 2013]. At this same site, Kowalewski [2007] conducted a 12 month study of two howler groups and reported that the best predictor of DPL was daily maximum temperature. Individuals in this study traveled greater distances on days in which temperatures exceeded 30°C, although during this same period the howlers were found to increase both time spent fruit eating and the number of different species of fruit consumed. Finally, although well documented cases of infanticide in howler monkeys are limited, it is possible that patterns of range use and DPL are influenced by the presence or proximity of lone adult males attempting to takeover a group. Thus, several factors may contribute to intra-annual variation in DPL in howlers.

In the present study, we examined factors affecting DPL in two neighboring groups of black and gold howler monkeys that were similar in group size and composition, and the effects that seasonal changes in food availability and distribution had on feeding competition and ranging behavior. Our goals were as follows: (i) to calculate each group's DPL during the spring (3 months) and summer (3 months). A comparison across this 6-month period enabled us to minimize the effects of day length on seasonal changes in activity budget and DPL (day length at our study site varies from 14 hr in summer to 10 hr in winter) and (ii) to examine how variation in diet, patch size and distribution, frequency of intergroup encounters, and mean daily temperature affected DPL. We predicted that: (P1) DPL will increase as the time spent feeding on discontinuous or scattered food patches increases, and DPL will decrease as the time spent feeding in food patches that exhibit a uniform or clumped distribution increases; (P2) DPL will increase as the availability of discontinuous or scattered food patches increases, and DPL will decrease as the availability of continuous or clumped food patches decreases; (P3) when exploiting food resources distributed within the crown of a single tree, group spread in howlers is expected to decrease and aggression over food increase, whereas when exploiting resources distributed across the crowns of several neighboring trees, group spread is expected to increase and opportunities for feeding competition are expected to decrease; (P4) on days in which groups engage in intergroup encounters in response to the howling of neighboring groups, DPL is expected to increase as individuals travel to the borders of their home range; and (P5) under conditions of high daytime temperatures (heat stress), howlers are expected to increase time spent resting and decrease DPL as an energy conservation strategy.

METHODS

Study Area and Subjects

We conducted this study in a semi-deciduous gallery forest in San Cayetano (27° 30′S, 58° 41′W), located in the basin of the Riachuelo River, in the northwestern part of the province of Corrientes, Argentina (Fig. 1). The study area has 24 identified forest fragments that contain black and gold howler monkeys. Fragment size averages 9.24 ha, SD = 7.62 ($N = 24$ fragments), ranging in area from 1.4 to 29.3 ha. The average distance between fragments is 1,763.1 m, SD = 538.7 ($N = 11$ fragments) [Oklander et al., 2010]. The average annual temperature is 21.7°C. During this study the average daily temperature was 22.7°C (range 17.4–29.4°C). The lowest daytime temperature recorded was 6.9°C in September (minimum temperature average 17.4 ± 4.4°C) and the maximum temperature was 35°C in December (maximum temperature average 29.4 ± 5.3°C). Rainfall is approximately 1.230 mm per year [Zunino et al., 2007]. Daily rainfall and temperature were obtained from the National Weather Service at the Aero Corrientes station, which is located 17 kmN of the study site. We present data obtained from two fully habituated groups of black and gold howler monkeys (Ar and Ta groups). Home range overlap between these two groups was approximately 42%. In addition, the home range of Ar overlapped approximately 25% with that of neighboring group Ali. The home range of Ta overlapped approximately 50% with neighboring groups Ali and Le. Overall, approximately 90% of Ta's home range overlapped with the home ranges of other howler groups.

Individuals in our study groups were recognized by differences in body size, pelage coloration, scars, and artificial marks (ear tags and colored anklets) placed on the howlers during a program of trapping and marking, which was part of a previous study

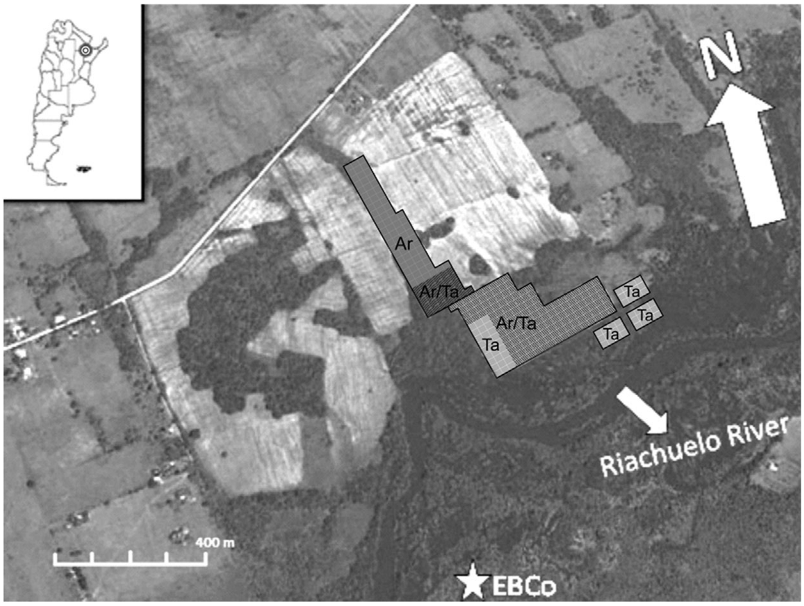

Fig. 1. Location of our study groups relative to EBCo (Biological Field Station Corrientes), the relativeposition of the forest fragments and the $20 \times 20\ m^2$ quadrats that the study groups used during this study(Ar: quadrats used only by group Ar, Ta: quadrats used only by Ta, and Ar/Ta: quadrats used by the twogroups).

conducted at this field site. The age and sex composition of each group were determined following the classification of Rumiz [1990]. Group Ar (five individuals) was composed of one adult male, one subadult male, one adult female, one juvenile male, and one infant male. Group Ta (six individuals) was composed of one adult male, one subadult male, two adult females, one juvenile female, and one infant female.

The two study groups were followed from sunrise to sunset for three complete consecutive days per month, from September 2007 to February 2008, completing a total of 463 hr of observations (230 hr of Ar and 233 hr of Ta). Spring (September–November) and summer (December–February) data collection ensured the inclusion of two seasons that differed significantly in the availability of fruits, flowers, new leaves, mature leaves, and buds. Each group was followed for between 13 and 14 hr/day. Behavioral data collection began when group members awoke in their sleeping tree in the early morning and ended when the monkeys entered a sleeping tree in the early evening, adopted their sleeping positions, and the following morning the group was found at the same tree.

Ecological Data, Phenology and Analysis of Seasonality of Resources

An area of approximately 10 ha, located in part of the forest that overlapped the home ranges of both study groups was selected for vegetation analysis (home range Ta = 6 ha, home range Ar = 5 ha). This area was subdivided into quadrats of $20 \times 20\,\text{m}^2$ (110 of these quadrats were located in the home range of Ar and 170 were located in the home range of Ta), with 80 quadrats located in the area of home range overlap between the two study groups. Within this area a total of 3,015 trees were mapped and identified with numbered plates. In each $20 \times 20\,\text{m}^2$ quadrat, we collected data on each tree, shrub, and vine with a diameter at breast height (DBH) ≥ 10 cm, the scientific name, DBH, maximum height (estimated using a clinometer), diameter and height of the crown, crown volume (calculated depending on crown shape using the geometric formulae for sphere, cone, quadrat, cylinder, hemisphere), and its precise location within the quadrat (each quadrat was subdivided into $16 = 5 \times 5\,\text{m}^2$ subquadrats to construct an accurate map of tree distributions). Based on these data, we calculated several ecological indices to characterize the habitat including tree species density (calculated as number of individuals of one species/unit area), frequency of that species within the group's home range, basal area or dominance (calculated as area at DBH/unit area), and importance value index (IVI, calculated as sum of relative density, relative dominance and relative frequency). The importance value index (IVI) varies form 0 to 100 with 0 indicating the least common species in the forest used by each study group and 100 indicating the most common plant species in the forest used by each study group [Dallmeier, 1992]. We also estimated the availability and seasonality of resources including ripe fruits, unripe fruits, young leaves, mature leaves, and flowers once per month by calculating phenological scores for plant species identified as food items in the diet of each group during the study. Each month, we monitored ten trees from each of the 25 plant species fed in by howlers for the presence and abundance of fruit, leaf, flower, and shoot phenophases. Each crown was subdivided into four parts, and the abundance of each phenophase (flowers, new and mature leaves, fruits) was ranked on a relative scale of 0–4, where 0 is the absence of that phenophase and 4 is when the crown is 100% in that phenophase ($0 = 0\%$, $1 = 25\%$, $2 = 50\%$, $3 = 75\%$). The phenological values of the individuals of each species were averaged to obtain a Phenological Index for that Species (PISp) for each month and for each phenophase. This value was weighted to calculate an index of abundance using Basal area (area of the tree at DBH/area unit) of the trees to determine seasonal variation of each phenophase (availability) [Kowalewski, 2007; Zunino, 1989]. An index of relative abundance (RAph index) was calculated for each plant species and phenophase per month. We estimated RAph using the formula: $\text{RAph} = \Sigma(\text{PIsp} \times \text{BAsp})$, where $\text{BAsp} = \text{basal area of species i/total basal area} \times 100$. The RAph index was used to calculate the monthly variation in resource availability and seasonal differences in the availability of fruits, flowers, and leaves of individual plant species [Placci, 1995]. Given the amount of home range overlap across groups, these data were pooled in all analyses.

Definition and Distribution of Food Patches

In this study, we consider a food patch as one or more interdigitated tree crowns that offer similar food items such as fruits, flowers, or leaves that was visited by the howlers during a feeding session. A food patch is then a unit of food type (fruits, flowers, or leaves) without considering the species of food consumed. A feeding session was considered a period of the day during which feeding was the predominant activity of all group members. Feeding sessions ranged in duration from 20 to 80 min (Group Ta 45 ± 17 min, Group Ar 47 ± 17 min). During this study, howler groups averaged four feeding sessions per day and each feeding session concentrated principally on a single type of food item, either fruits (including mature and immature), flowers, or leaves (including mature, and immature leaves, and shoots). We analyzed the distribution of these patches within the howler home ranges using several indices of dispersion. To assess patch distribution we calculated an Index of dispersion

(ID) of fruit, flower, and leaf patches as the ratio between the mean number of patches and its variance for each quadrat. An ID >1 indicates a clumped patch distribution, an ID <1 indicates a uniform distribution and an ID $=1$ indicates a random distribution. The frequency distribution for each food patch type was compared to a Poisson distribution and tested for significance using a Student's, *t*-test (using the formula $t = \left| s2/{-1} \right| / \sqrt{2/(\mathrm{n}-1)}$). We also calculated Morisita's ID (MID) to assess patch dispersion. A MID $=1$ indicates a random distribution, a MID >1 indicates a clumped distribution, and a MID <1 indicates a uniform distribution. To test for a significant deviation from 1 (random), a chi-square test was used.

Behavioral Data

Every 10 min, we recorded a 2 min scan sample [Altmann, 1974], in which we scored for each group member his or her vertical height in the canopy (measured using a clinometer), location (quadrat within the home range), tree/food patch ID, and activity (*travel*, movement within the crown of a tree or between the crowns of trees whose immediate goal in not to consume a food item or to interact socially with a conspecific; *rest*, a period of inactivity lasting at least 60 sec; *feed*, when an individual was manipulating or ingesting a food item or drinking water from a site located in a tree or small stream; and *social interactions*, which include play, grooming, displacement, fighting, chasing, threatening, or howling). During each scan sample, we recorded the identity and distance of the nearest neighbor in such a way that we could construct a "map" of the position if each individual in the group. We calculated group spread with this "map" every 10 min, which was defined as the area of a circle (πr^2) with a radius (r) that was estimated as the distance between the farthest individual to the imaginary center position of the group. In addition, during each observation minute we identified the location of the tree in which most of the group was located (more than 50% of the group) and plotted that tree on a map of the field site. If individuals were spread out such that no tree contained more than 50% of the group we identified a point as the estimated center location to all group members and plotted that point onto the field map. DPL was calculated directly by measuring, with a meter tape, the horizontal straight-line distance (trunk to trunk at breast height) between sequentially visited trees. Measurements were taken the day after the 3-day behavioral data collection period was completed. To estimate the amount of each food type consumed (in grams), we first converted the data on percentage of the activity budget devoted to feeding into feeding minutes following van Doorn et al. [2010]. Second, following Garber et al. [2015], we used the average feeding rates for each food type (e.g., ripe fruits, unripe fruits, immature leaves, mature leaves, flowers) based on published studies of *A. seniculus* and *A. pigra* to transform the data on time spent feeding into an estimate of the amount (in grams) of each fresh food type consumed. We used a Spearman's correlation to identify an association between DPL and the amount of each food type consumed.

Statistical Analysis

We used linear mixed modeling [Package: nlme, version 3.1–120, Pinheiro & Bates, 2000; Pinheiro et al., 2014] to evaluate the relationship between DPL and variables associated with feeding behavior, diet, activity budget, group spread, intergroup encounters, mean daily temperature, and indices of food availability and distribution (see Table I for a detailed description of predictive ecological variables). This method offers advantages over more traditional data analysis methods by quantifying the variation among sampling units, such as variation among individuals (when multiple responses are measured per individual, for example, the survival of multiple offspring or sex ratios of multiple broods) [Bolker et al., 2009; Zuur et al., 2009]. The random effect was group identity (two groups, Ar and Ta). The response or dependent variable was DPL (Table I), which was log-transformed to meet model assumptions (normal distribution of errors and homogeneity of variances).

In order to detect and minimize problems associated with multicollinearity, correlations

TABLE I. Description of Variables Used in the Linear Mixed Model. DPL, Is the Response or Dependent Variable; the Other Behavioral and Ecological Variables Were Associated With DPL Based on the Results of PCA and Linear Modeling

Variables	Description
DPL	DPL (meters)
Tmean	Mean daily temperature (°C)
Tmax	Maximum daily temperature (°C)
Tmin	Minimum daily temperature (°C)
Trange	Daily temperature amplitude (°C)
RAphShoot	Relative abundance of shoot
RAphNL	Relative abundance of new leaves
RAphML	Relative abundance of mature leaves
RAphFlower	Relative abundance of flower
RAphIF	Relative abundance of immature fruit
RAphMF	Relative abundance of mature fruit
Tshoot	Time invested feeding on shoots
tNL	Time invested feeding on new leaves
tML	Time invested feeding on mature leaves
tflower	Time invested feeding on flowers
tIF	Time invested feeding on leaves
tMF	Time invested feeding on mature leaves
Nencounters	Number of encounters between two groups
Dispersion	Group dispersion (cm)

between ecological variables were evaluated via the Pearson correlation coefficient. Because many of these variables were highly correlated ($r \geq 0.6$ or ≤ -0.6, Appendix 1), we used principal components analysis (henceforth, PCA) to obtain independent measures of predictive variables, and to reduce the number of predictive variables in the statistical model. PCA is a multivariate ordination technique that represents a data set containing several variables (Table I) as a data set with a smaller number of composite variables, the components or axes of the PCA. These axes are orthogonal, that is, they are uncorrelated, and represent the strongest covariation patterns among the variables in the original data set [McCune et al., 2002] (Table II). Based on these criteria, principal components 1–8 were chosen to represent variation in the original ecological parameters and as predictive variables in the linear mixed model. To evaluate model assumptions of normality we used a modified Shapiro–Wilks test, and this assumption was met ($W = 0.95$, $P = 0.36$). To test for homogeneity of variances, we inspected a residual plot (predicted values vs. residuals), and this plot showed homogeneity of variances. All analyses were conducted in Infostat [Di Rienzo et al., 2011] and R Version 3.0.3 [R Development Core Team, 2014]. This research is part of larger populational study of the behavior, ecology, and demography of *A. caraya* in Northern Argentina and complied with the American Society of Primatologists principles for the ethical treatment of human primates, the University of Illinois, Urbana guidelines for animal research, and the laws of Argentina (IACUC protocol 06207).

RESULTS

Diet and Activity Patterns

Over the course of 36 complete observation days, we obtained 5,138 focal animal scans for Group Ar and 6,365 focal animal scans for Group Ta (total 11,503 scans, and 463 hr of observation). Both groups had similar activity patterns (Resting Ar = 53% Ta = 60%, Traveling Ar = 12% Ta = 13%, Feeding Ar = 27% Ta = 21%, Social Interactions Ar = 8% Ta = 6%). Within each group, we found no evidence of seasonal changes in activity budget (Fig. 2) (Kruskal–Wallis ANOVA test: $H = 1$, $P > 0.05$, $N = 12$).

Figure 3 indicates the percentage of each food phenophase ingested per month for members of each group, and reveals a similar dietary emphasis (Kruskal–Wallis ANOVA test: $H = 1$, $P > 0.05$, $N = 12$). Combining data on feeding time for both howler groups during the 6-month study period, individuals devoted 35% of feeding time to consuming mature fruits, 16% to immature fruits, 31% to new leaves, and 13% to mature leaves. However, there was evidence of marked seasonal differences in howler feeding patterns. Combining the data from both groups, in spring new leaves (33%), mature leaves (17%), immature fruits (16%), mature fruits (17%), and flowers (10%) were the most common items in the howler diet, whereas during the summer (Fig. 3) howlers increased time devoted to the consumption of mature fruits (54%) and decreased their consumption of new leaves (29%), mature leaves (10%), immature fruits (7%), and flowers (0%) (Fig. 3). New leaves were eaten during all

TABLE II. Results of the Principal Components Analysis. The Values Are Pearson Correlation Coefficients Between the Original Ecological Variables and Principal Components

% explained variance	0.33	0.18	0.16	0.08	0.07	0.05
Variables	PC1	PC2	PC3	PC4	PC5	PC6
Tmean	**0.57**	**0.71**	−0.34	0.05	−0.01	0.02
Tmax	*0.46*	**0.81**	−0.18	0.21	−0.07	0.18
Tmin	**0.66**	**0.58**	*−0.39*	−0.13	−0.05	−0.11
Trange	−0.14	**0.58**	0.24	*0.55*	−0.05	0.47
RAphShoot	*0.50*	0.04	**0.60**	−0.23	0.36	0.01
RAphNL	**0.56**	0.25	**0.72**	−0.03	0.07	−0.06
RAphML	0.73	*−0.48*	−0.37	0.08	0.12	0.16
RAphFlower	*−0.46*	*0.54*	**0.64**	−0.09	−0.09	−0.04
RAphIF	**0.80**	−0.31	0.05	0.04	0.33	−0.03
RAphMF	**0.81**	−0.34	−0.20	0.06	−0.01	0.13
tshoot	*−0.55*	−0.36	−0.06	0.12	0.33	0.52
tNL	*−0.44*	0.36	−**0.63**	−0.11	0.26	−0.19
tML	−**0.69**	0.18	*−0.43*	−0.22	0.25	0.03
tflower	−**0.61**	−0.23	0.34	−0.21	-0.30	0.12
tIF	0.11	0.28	*0.44*	−0.18	**0.63**	−0.01
tMF	**0.69**	−0.12	0.26	−0.24	−0.44	0.06
Nencounters	0.27	−0.32	0.12	**0.75**	0.08	−0.29
Dispersion	−**0.59**	0.06	0.20	*0.50*	0.06	−0.31

Variables in bold have correlations higher than or equal to ± 0.6, and variables in italics have correlations higher than ± 0.55 and lower than ± 0.60.

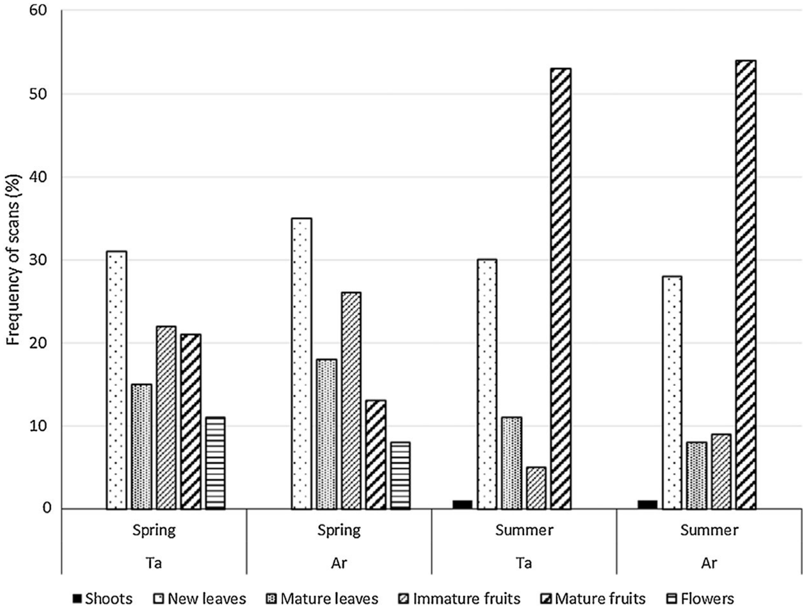

Fig. 2. Seasonal diet composition of each howler group (September 2007 to February 2008).

months of the study, accounting for approximately 30% of feeding time per month. A Spearman correlation examining the IVI (Importance value index) of food species and the percentage of each species in the diet indicated no clear association ($N = 17, R = 0.26, P = 0.32$). Thus, the howlers did not consume the most highly available food resources in their home range. Rather, both the plant species composition of the howler diet and the food types consumed indicate a pattern of selectivity with plant species such as *Eugenia uniflora* (fruits), *Ficus luschnathiana* (fruits), and *Clorophora tinctoria* (fruits) serving as preferred taxa.

The average group spread for Ta was $120 \pm 80\,\mathrm{m}^2$ and for Ar was $80 \pm 40\,\mathrm{m}^2$, suggesting that during all months of the year and across all activities, groups were highly cohesive. During the entire study period, we recorded a total of only four instances of within-group agonistic interactions during feeding. In each case the event occurred in a fruit patch and involved only adult males. This resulted in a rate of 0.03 agonistic interactions/hr/indiv during feeding.

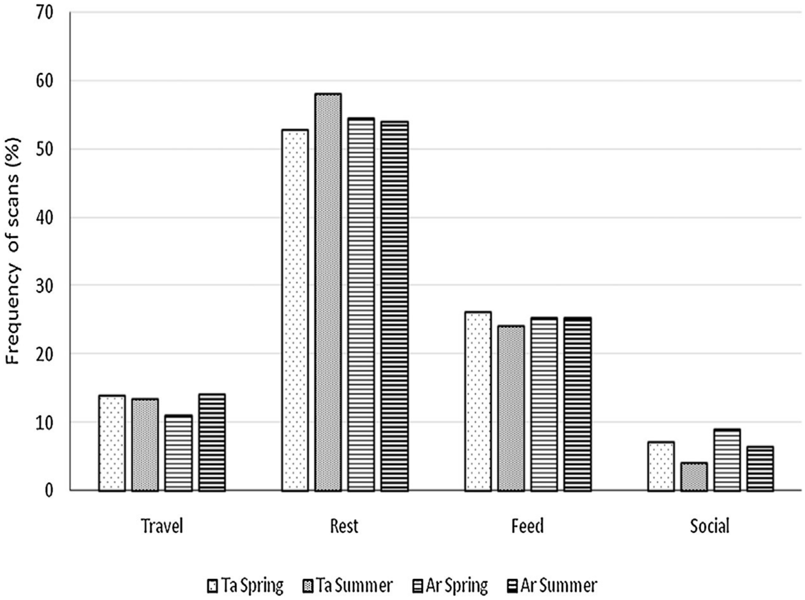

Fig. 3. Seasonal variation in the activity budget of each howler group (September 2007 to February 2008).

Patch Distribution

Based on two indices of resource dispersion, ID (Index of Dispersion) and MID (Morisita's Index of Dispersion), fruit patches and flower patches exploited by the howlers exhibited a scattered distribution compared to leaf patches, which exhibited a more uniform distribution across each group's home range (IDfruit patches = 1.22, IDflower patches = 1.37, and IDleaf patches = 0.44 ($P < 0.05$) and MIDfruit patches = 1.1, MIDflower patches = 2.24, and MIDleaf patches = 0.75 ($P < 0.05$). This also is supported by data on interpatch distance. The distance between fruit patches (average = 300 ± 90 m, $N = 25$) and the distance between flower patches (average = 225 ± 40 m, $N = 4$) was considerably greater than distance between leaf patches (average = 139 ± 67 m, $N = 12$) exploited by the howlers. We found that DPL varied between seasons (greater in summer when ripe fruits dominated the diet and lower in spring when leaves dominated the diet) but were similar between groups (DPLTa-Spring = 673 ± 177 m; DPLAr-Spring = 673 ± 172 m; DPLTa-Summer = 850 ± 117 m; DPLAr-Summer = 870 ± 106 m) (Mann–Whitney: $U = 151$, 50, $P = 0.739$, $N_{1,2} = 18$, 18) (Fig. 4).

Predictive Variables of DPL

The predictive variables in the linear models were the first six PCA axes, which accounted for approximately 94% of the variance in the original data matrix. In each model, there was a correlation ≥ 0.4 with at least one of the original ecological variables (Table II). Our model accounted for 82% of variance in the response variable ($R^2 = 0.82$) and the results are shown in Table III. The principal components (PCs) that were significantly associated with DPL (data for both groups combined) were PC1, PC2, and PC3 ($\alpha = 0.05$; P for PC1 = <0.0001; P for PC2 = 0.007; P for PC3 = 0.03). PC1 (33% explained variance) described a contrast between variables with high values (>0.6) of RAphMF, RAphIF, RAphML, RAphNL, tMF, Tmin, and Tmean, and low values (<-0.6) of tML, tflower, and group dispersion (see Table I for a definition of these variables). Overall, these results indicate that under conditions of high immature and mature fruit availability the howlers increased DPL whereas the increased availability and increased time invested in feeding on mature leaves resulted in a decrease in DPL. This is consistent with the expectations of Prediction 1 and Prediction 2, namely that DPL will increase when exploiting scattered food patches (fruit) and decrease when exploiting clumped or uniformly distributed food patches (leaves). In addition, we found that group spread increased up to 4,000 m^2 when howlers exploited leaf patches (a single leaf patch included 4–10 quadrats) compared to fruit patches (0.5–4 quadrats). However, given the limited instances of contest competition at feeding sites ($N = 4$) there was no evidence of increased aggression when feeding on clumped resources. Thus Prediction 3 was not supported. Moreover, with increased group spread, there was a decrease in DPL (Table II) providing further support for our observations that with an increase in leaf eating, howlers traveled shorter distances per day.

TABLE III. Results of the Linear Mixed Model. Principal Components One With Three Were Significantly Associated to DPL ($\alpha = 0.05$)

	Value	Std. error	t-value	P-value
PC1	**0.086**	**0.009**	**9.24**	
PC2	**−0.037**	**0.013**	**−2.92**	**0.007**
PC3	**0.031**	**0.013**	**2.36**	**0.026**
PC4	0.035	0.019	1.89	0.071
PC5	0.014	0.020	0.67	0.509
PC6	0.040	0.025	1.61	0.119

Note: Specification of model in R (nlme package): modelo.003_LN_DDm_REML<lme(LN_DDm∼1 + CP.1 + CP.2 + CP.3 + CP.4 + CP.5 + CP.6 + CP.7 + CP.8, random = list(grupo = pdIdent(∼1)), method = "REML,"control = lmeControl(msMaxIter = 200), na.action = na.omit, data = R.data03, keep.data = FALSE). Our model accounted for 82% of variance in the response variable ($R^2 = 0.82$).
In bold significant Principal Component axes.

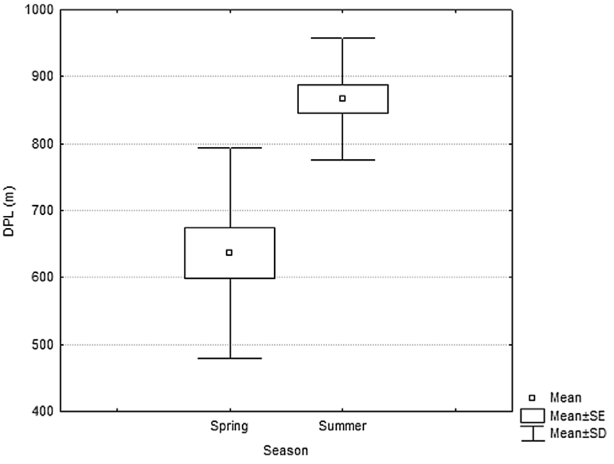

Fig. 4. Relationship between DPL (data for both groups combined) and spring and summer.

We found that PC3 (16% explained variance) was positively associated with RAphNL, RAphFlower, RAphShoot, and negatively associated with tNL. Thus, DPL increased with an increase in the availably of new leaves, shoots and flowers, and decreased when the time spent feeding on new leaves was highest. Given that time spent feeding is not a direct measure of the amount of food consumed because it includes both time devoted to handling and processing (manually and orally) each item, we explored the association between the estimated amount of each food type ingested and DPL. We found a positive association between DPL and the amount of mature fruits consumed ($N = 36$, $r = 0.6$, $P < 0.05$), and a negative association between DPL and the amount of new leaves ($N = 36$, $r = -0.4$, $P < 0.05$) and mature leaves ($N = 36$, $r = -0.5$, $P < 0.05$) consumed. Thus using measures of time spent feeding per food type multiplied by the amount consumed per unit time from the published literature on howlers, offers additional support that DPL decreased with an increase in the amount of leaves in the howler diet and DPL increased with an increase in the amount of fruit consumed by the howlers.

PC4 through PC8 were not significant. Therefore, we found no statistical support for Prediction 4. An increase in intergroup encounters was not associated with an increase in DPL (see PC4 in Tables II and III). However, we note that on days in which howlers engaged in intergroup encounters, day range increased approximately 220 m (average $\text{DPL}_{\text{days with encounters}} = 850 \pm 120$ m, $N = 15$ days; average $\text{DPL}_{\text{days without encounters}} = 630 \pm 195$ m, $N = 21$ days). Given that 50% ($N = 15$) of intergroup encounters in our howler study groups occurred during the breeding season, it appears that additional factors such as female fertility are likely to have contributed to DPL.

We also explored the possibility that temperature affected howler DPL. PC2 (18% explained variance) was strongly associated with daily Tmean, Tmax, Tmin, and Trange, indicating that on days in which maximum, minimum, mean daily temperatures were high, DPL increased. For example, on days in which the minimum temperature was greater than 20°C ($N = 12$), DPL was 790 ± 181 m, whereas on days in which the minimum temperature was below 10°C ($N = 5$), DPL was 562 ± 120 m. These results failed to support Prediction 5 that these howlers were using an energy conservation strategy on very hot days. The positive association between temperature and DPL also is supported by PC1, and we suggest that this relationship is best explained in terms of food availability driving howler movement and ranging patterns and temperature possibly associated with season affecting food availability.

DISCUSSION

Models of primate socioecology have tended to emphasize the importance of feeding competition in shaping many aspects of grouping patterns, within-group social interactions, and ranging behavior [Clutton-Brock & Janson, 2012; Snaith & Chapman, 2007; Sterck et al., 1997]. However recent critiques of these models indicate that evidence of feeding competition resulting in fitness costs is limited in many populations, and that under a wide range of social and ecological conditions individuals are able to flexibly adjust their activity budget, foraging strategies, ranging patterns, and social interactions to obtain sufficient resources [Chapais, 2006; Dias & Strier, 2003; Fan et al., 2014; Janson, 2000; Sussman & Garber, 2011; Thierry, 2008]. In the present study, we examined the set of factors that affect daily path length (DPL) in black and gold howler monkeys (*Alouatta caraya*). In this howler population both predation risk and infanticide risk appear to be relatively low. Based on observations of our study population conducted over the past 9 years, we have documented ten cases of observed or suspected infanticide in 22 howler groups (220 group years). This represents less than 2.5% of infants born during this period ($N = 387$ infants born). Each of these ten cases was associated with a male takeover, and in two cases we found the dead infant. In contrast most infant deaths over the same period were attributable to other causes (maternal condition, droughts—spring-summer 2007, predators—two cases in which a dog attacked a mother carrying her infant while traveling on the ground, parasitic infections, although the cause of most infant deaths remains unknown). Thus, although infanticide occurs occasionally in our population and we have no evidence to support the contention that infanticide risk was a primary factor in howler range use and movement patterns.

Increased DPL has previously been used as a proxy for increased feeding competition and the costs to individuals of traveling to additional feeding sites [Gillespie & Chapman, 2001; Janson & Goldsmith, 1995; Stevenson, 2006]. Our two study groups were similar in size (5–6 individuals), had overlapping home ranges, and based on observations collected over the course of 6 months, aggressive contests at feeding sites were rare and occurred at a rate of 0.03 events/individual per hour of feeding. This low rate of within-group aggression at feeding sites is consistent with other howler studies. In this regard, Kowalewski [2007] reported a rate of 0.003 agonistic interactions per individual per day in a study of two groups of *A. caraya* during a period of 12 months, and a rate of <0.004 aggressive interactions per hour per individual during feeding. Similarly low rates of within-group aggression have been reported in *A. palliata* (≈0.007 aggressive interactions per individual per hour [Jones, 1980]) and *A. seniculus* (≈0.0005 aggressive interactions per individual per hour [Rumiz, 1992]). Given small group size and limited evidence for feeding competition in the present study, we examined how patch distribution, patch availability, food type, group spread, intergroup encounters, and temperature affected DPL.

Our results indicated that an increase in the availability of ripe fruits, time invested in feeding on fruits, and the amount of fruits consumed had the strongest effect on increasing DPL in black and gold howlers. This appears to reflect the fact that within the home ranges of our study groups, fruit patches were discontinuous and more widely scattered (greater interpatch distance) than flower or leaf patches exploited by howlers. DPL also was positively correlated with the availability of new and mature leaves (PC1). However we did not find a strong association between DPLs and number of leaf feeding trees visited per day (Spearman $N = 36$, $r = -0.15$, $P > 0.05$). Thus, although the howlers frequently switched among different leaf species, possibly in an attempt to minimize the accumulated ingestion of secondary compounds present in a given leaf species [Dai et al., 2014; DeGabriel et al., 2009], the relatively uniform distribution of leaf patches did not result in an increase in DPL. We did find a positive association between the number of trees exploited for leaves and the number of trees exploited for fruits on the same day (Spearman $N = 36$, $r = 0.4$, $P < 0.05$) suggesting that the scattered distribution of fruit trees contributed to increased distance traveled [Garber et al., 2015].

PC1 and PC3 indicated a positive relationship between DPL and the availability of flowers but a negative relationship with time spent feeding on flowers. We also found a negative associations between time spent feeding on flowers and the estimated amount of flowers ingested (Spearman $N = 36$, $r = -0.35$, $P < 0.05$) with DPL. Given the scattered distribution (average interpatch distance of 225 m) of neighboring flower feeding sites, we expected that howlers would travel greater distances on days in which flower consumption increased. This was not the case. We note, however, that the howlers consumed flowers on only 10 of 18 observation days during the spring and did not feed on flowers during the summer. On days in which flowers were exploited, they visited an average of 3 ± 1.7 trees per day (and between 2 and 3 vine patches). The most common flower species consumed was *Myrcianthes pungens*. An average of 5 ± 1 *M. pungens* trees were visited on each of 6 days. This species was characterized by an interpatch distance of only 70 ± 25 m, and this may help explain why DPL did not increase during days of increased flower feeding.

The positive association between DPL and the availability of new leaves (but not mature leaves) appeared to be driven principally by the relationship between DPL and fruit availability (See PC1 in Table II, Fig. 5). Seasonal variation in the amount of time spent feeding on immature leaves was minimal (33% of feeding time in spring vs. 29% of feeding time in the summer), and DPL was negatively associated with both time spent feeding on new leaves and with the estimated amount of new leaves ingested. Therefore increased DPL during the summer appears to have been driven primarily by the howler preference to exploit fruit patches that were discontinuous and scattered across their range.

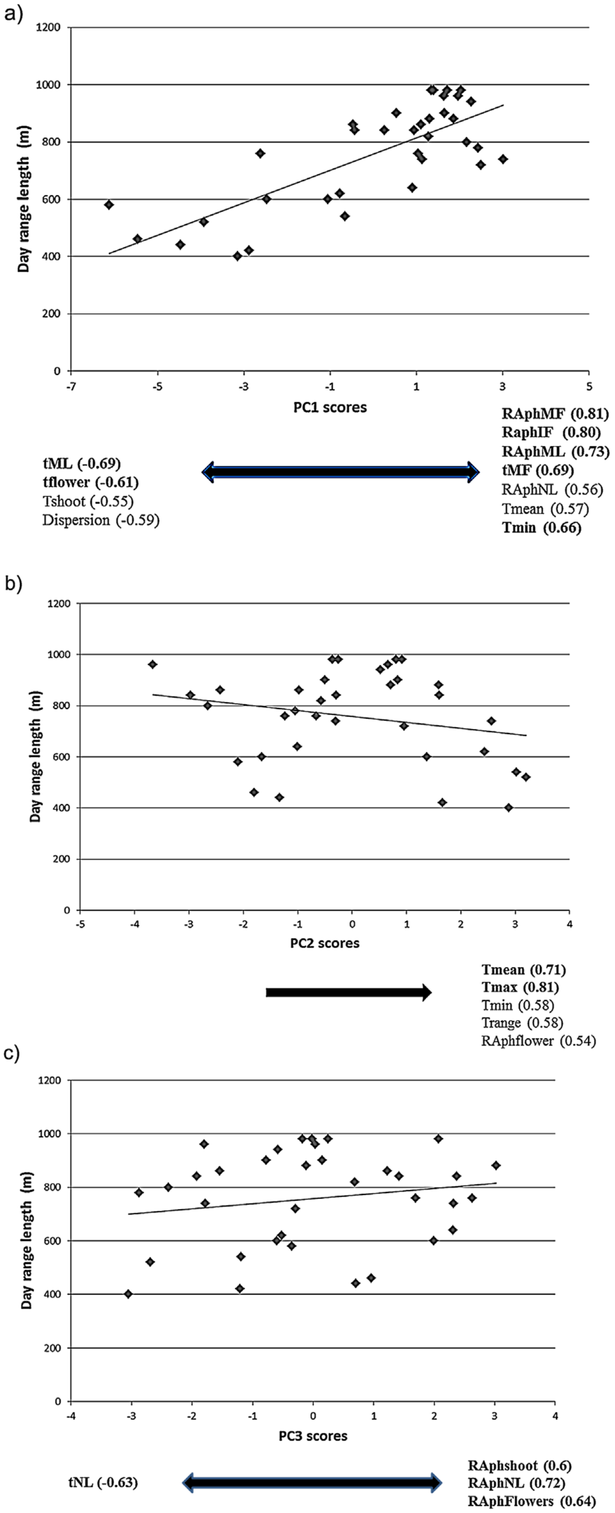

Fig. 5. Relationship between day range (m) and significant PC1 scores (**a**), PC2 scores (**b**), and PC3 scores(**c**). Numbers in parentheses are Pearson correlations between each variable and PC1, PC2, and PC3 scores.Variables in bold have correlations higher than or equal to ±0.6, and variables in italics have correlationshigher than ±0.55 and lower than ±0.60.

Predictions 3–5 were not supported. We did not find an increase in aggression or a change in group spread when the howlers exploited foods located in a single tree crown (P3), nor did DPL increase on days in which groups engaged in intergroup encounters (P4). In addition, our results indicated that under conditions of high daytime temperatures (potential heat stress), howlers did not increase time spent resting nor did DPL decrease as a means to conserve energy during high summer temperatures. However, even on hot days in which the howlers increased DPL, the additional distances traveled were on the order of only 50–200 m per day. Data on the energetic cost of travel in both arboreal and terrestrial primates indicate that traveling an additional 50–200 m accounts for less than 0.05–0.2% of total daily energy [Steudel, 2000]. We conclude, therefore, that monthly variation in DPL during our study was not of sufficient magnitude to result in a significant increase in energy requirements or a noticeable change in activity budget.

Fruits represent an easily processed food that, in addition to contain simple sugars, may be relatively high in lipids (lipids contain twice the metabolizable energy per unit than protein or carbohydrates) [Conklin-Brittain et al., 2006]. In a detailed study of the nutritional composition of food items consumed by howlers at our site, Fernández [2014] found that although the lipid content present in leaves, flowers, and ripe fruits was generally low (1.5–2.7%), immature fruits contained 8.6% lipids. Similarly, Righini et al. [2016] found that the lipid content of ripe (11.1%) and immature fruits (5.4%) consumed by black howlers (*A. pigra*) in Mexico was greater than the lipid content of young leaves (1.9%) and mature leaves (2.4%). Thus, the relatively small energetic costs of traveling an additional 200 m per day to acquire fruit during the summer, even when daytime temperatures reached 35°C, appeared to be compensated by increased access to a high energy resource.

Finally, opportunities for scramble competition have been argued to increase during periods of resource scarcity, as individual group members spread out to locate and consume small and scattered food patches. This is expected to result in a decrease in group cohesion and an increase in DPL if individuals visit additional feeding sites to satisfy their nutritional and energy requirements [Chapman & Chapman, 2000; Snaith & Chapman, 2007]. However, this was not the case in black and gold howlers. Group spread averaged only $200 \pm 152\,m^2$ across all feeding conditions was smaller during fruit feeding than during leaf feeding and did not increase when exploiting feeding sites of lower productivity.

In conclusion, our results suggest that DPL in black and gold howlers is influenced by several interrelated factors. An increase in DPL in our study was primarily driven by fruit availability and fruit consumption. During periods when fruits were most available (summer) the howlers increased time spent feeding on mature fruits (from 17% of feeding time in spring to 54% of feeding time in summer and from $1{,}006.0 \pm 753.6\,g$ fresh weight in spring to $1{,}675.8 \pm 802.8\,g$ fresh weight in summer) resulting in an average increase in DPL of approximately 200 m. Although many researchers have characterized howlers as folivores and highlighted their ability to exploit difficult to digest foods when fruits and flowers are unavailable [Glander, 1981; Milton, 1980], a recent review by Garber et al. [2015] indicates that many species of howlers consume both a fruit-enriched or balanced fruit and leaf diet [Amato & Garber, 2014; Fernández, 2014; Righini, 2014]. Thus, as is the case for other atelines, fruits represent a critical component of the howler diet accounting for 50% or more of the total amount of food ingested [Garber et al., 2015]. Given evidence that feeding competition plays a relatively limited role in the feeding ecology and social interactions of *A. caraya* and several other howler species [Wang & Milton 2003], models of socioecology and ecological constraints [Chapman & Chapman, 2000; Clutton-Brock & Janson, 2012; Reichard & Nowak, 2010; Snaith & Chapman, 2008; Sterck et al., 1997; Sussman & Garber, 2004, 2007] need to reconsider how factors such as individual nutritional requirements, social tolerance and group cohesion, and the spatial and temporal availability of preferred and nearby food resources influence primate social and ranging behavior.

ACKNOWLEDGMENTS

We thank Anthony Di Fiore and two anonymous reviewers for their comments that help to improve this manuscript. We thank the support of Dr. Gabriel Zunino during the field work and for stimulating discussions on the topic. We thank Maria Wollnik for constructive comments on earlier drafts of this manuscript. We also thank our field assistants and collaborators: Mariela Martinez, Cecilia Allen, Marina Maiden Ferrucci, Valeria Colombo, Gabriela Ballesteros, and Ramon Martinez. We finally thanks to Mariana Garcia, for her help with the changes in the map of this manuscript. This work was supported by the Scott Neotropical Fund of The Cleveland Zoological Society and Cleveland Metroparks Zoo (MK) and PIP IU 355/CONICET-Argentina (MK). The study complied with the current laws and permission of the United States and Argentina (IACUC protocol 06207), and adhered to the ASP principles for the ethical treatment of nonhuman primates. PAG thanks Chrissie, Sara, and Jenni for their love and support.

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