

# Effects of Lactation on the Time-Budgets and Foraging Patterns of Female Black Howlers (*Alouatta pigra*)

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**ABSTRACT** Lactation is an energy demanding phase in the reproductive cycle of female mammals. For this reason, several studies have assessed the effects of lactation on female behavior. In this study we examine the influence of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*) in Campeche, Mexico. We observed 32 adult females and 35 infants belonging to 14 groups of black howlers for a total of 2,224 focal hours. We found that lactating females spent more time being inactive and feeding from fruits than nonlactating females. In addition, during the first two-thirds of lactation females were more active (i.e., rested less, fed more, devoted more time to social activities, and moved more) and foraged more intensively (i.e., ranged over larger distances, used more feeding trees and feeding species, and consumed more leaves)

than females in the last third of lactation. Lactation seems to force black howler females to reduce activity and to maximize the intake of high-quality foods, with inactivity being the highest during late lactation, when females probably face the cumulative effects of nursing older infants and of a new pregnancy. Early lactation is probably the most energetically demanding stage of lactation for black howler females. This study demonstrates that despite being energetically constrained by a highly folivorous diet, reproductive state affects several dimensions of the behavior of black howler females. Therefore, variation in time-budgets and foraging strategies of howlers has been probably underestimated by previous research that has not considered physiological differences among individuals. *Am J Phys Anthropol* 145:137–146, 2011. © 2011 Wiley-Liss, Inc.

Lactation is a critical phase in the reproductive cycle of female mammals, as it is an energetically demanding and relatively inefficient activity (Gittleman and Oftedal, 1987; Loudon and Racey, 1987; Clutton-Brock, 1991). It has been estimated that female mammals increase caloric intake by 66–188% during lactation (Gittleman and Thompson, 1988). As a result of higher caloric demand, lactating females may present a loss in body weight (Laurenson, 1995), an increase in vulnerability to disease (Lloyd, 1983; Festa-Bianchet, 1989), or an increase in mortality rates (Altmann and Alberts, 2005).

To maintain their metabolic balance, primate females have been reported to display a number of behavioral adaptations during lactation, such as increases in feeding time (Altmann, 1980; Koenig et al., 1997), quantity (Sauther and Nash, 1987; McCabe and Fedigan, 2007), or quality (Boinski, 1988; Sauther, 1994; Murray et al., 2009), or reduction in activity levels (Harrison, 1983; Dunbar and Dunbar, 1988; Barrett et al., 2006; Piperata and Dufour, 2007). These behavioral adaptations vary throughout lactation as a function of infants' age and energy requirements, and of the costs of maternal care (e.g., transportation, vigilance). For example, time spent feeding by lactating yellow baboon (*Papio hamadryas cynocephalus*: Altmann, 1980) and gelada (*Theropithecus gelada*: Dunbar and Dunbar, 1988) females increases throughout lactation, whereas among siamangs (*Symphalangus syndactylus*) females spend more time feeding during early lactation than during the later stages of infant care (Lappan, 2009). Among chacma baboons (*P. h. ursinus*) and some human cultural groups (*Homo sapiens*), lactating females reduce activity levels during the first few months, relative to later months, post-partum (Barrett et al., 2006; Piperata and Dufour, 2007).

Concerning dietary adaptations, among white-faced capuchins (*Cebus capucinus*: McCabe and Fedigan, 2007), vervet monkeys (*Chlorocebus aethiops*: Lee, 1987) and chimpanzees (*Pan troglodytes*: Murray et al., 2009), lactating females consume more high-quality food items (i.e., food that is high in energy and nutrients). In the first two species, the intake of high-quality foods by lactating females increases steadily from birth until infants begin to walk independently, and then decreases until weaning, suggesting that transportation costs constrain female diets. Lactating white-faced capuchin females also ingest more food items than nonlactating females (McCabe and Fedigan, 2007). Among siamangs, however, females do not shift their diet to higher-quality food items during lactation to offset energy expenditure (Lappan, 2009).

There is also evidence that lactating females adjust their behavior to the energetic demands of lactation through a trade-off between time-budget components.

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Among geladas, during the first stages of lactation females increase feeding time at the cost of resting (Dunbar and Dunbar, 1988), and lactating chacma baboon and gelada females, for instance, reduce social time when feeding time increases (Dunbar and Dunbar, 1988; Barrett et al., 2006). Furthermore, during the first four months of infant life, chacma females increase vigilance to avoid infanticide at the cost of feeding, and the proportions of time dedicated to resting and vigilance maintain a positive relationship (Barrett et al., 2006). Therefore, conspecific threats are an important additional constraint on the behavior of lactating females, especially during the early stages of lactation, when the probabilities of infanticide are higher (van Schaik, 2000). Finally, in some human groups, reductions in time spent foraging by lactating women (e.g., processing foods) are followed by increases in time spent inactive (Piperata and Dufour, 2007).

Folivorous primates have long been considered to be energetically constrained by the low caloric content of their foods and, as a consequence, to show little variation in their time-budgets and foraging behavior (e.g., Milton, 1998). Therefore, in contrast with generalist (e.g., chacma baboons: Barrett et al., 2006; white-faced capuchins: McCabe and Fedigan, 2007) or frugivorous (e.g., chimpanzees: Murray et al., 2009; siamangs: Lappan, 2009) female primates, the behavior of folivorous female primates should not vary significantly throughout their reproductive cycles. Although this has not been tested directly in primate studies, there is some evidence against this prediction. Despite being primarily folivorous, female geladas do modify their behavior throughout lactation, mainly through adjustments in time-budgets as discussed above (Dunbar and Dunbar, 1988). Furthermore, it is possible that variation in time-budgets and foraging behavior of folivorous primates has been underestimated, as traditionally the effects of female reproductive state have not been analyzed (e.g., Matsuda et al., 2009). In the present study we address these questions by investigating the behavior of female black howlers (*Alouatta pigra*) during lactation.

Black howlers live in permanent social groups, usually composed of one to three adult males, one to three adult females and their offspring (Van Belle and Estrada, 2006). Although howlers are nonseasonal breeders (Crockett and Eisenberg, 1987), in Belize there is a cluster of births during those months when rainfall is lowest (i.e., dry season: December–May; Brockett et al., 2000). In this species, males provide only indirect parental care (e.g., bridging during travelling, vigilance and protection against conspecifics and predators: Bolin 1981; Treves et al., 2001; Kitchen, 2004). Female sexual cycles last about 18 days (Van Belle et al., 2009), and preliminary observations for *A. pigra* populations living in Campeche (Yucatan Peninsula, Mexico) indicate that the average interbirth interval when the previous infant survives is ~15.5 months ( $\pm 4.3$  SD,  $N = 8$  females; Rangel-Negrín et al., 2009), and that lactation lasts ~14 months (Rangel-Negrín and Dias, unpublished data).

The presence of dependent immatures affects female social behavior in this species. First, females with immatures (i.e., 0–36 months) spend more time vigilant than females without immatures, and mothers of immatures of 0–12 months are more vigilant than mothers of immatures of 12–36 months (Treves et al., 2003). Second, females living in groups with small immatures show less intense responses to simulated intruders (by approaching

speakers) than those in groups without small immatures (Kitchen, 2006). There is no evidence suggesting that younger infants are more vulnerable to predation than older immatures. However, infanticide in howlers usually occurs during the first 3 months of life (Crockett, 2003); thus, vigilance to prevent potentially infanticidal attacks during early lactation may represent a major constraint on female behavior.

Because of their folivorous-frugivorous diet and lack of a specialized digestive system (Milton, 1980), *Alouatta* evolved an energy-minimizing strategy, which is primarily characterized by long periods of inactivity (Di Fiore and Campbell, 2007), a flexible diet, high selectivity of food items (Glander, 1978; Milton, 1979, 1980), and goal-directed travel that minimizes time spent traveling and ranging distances between food sources (Garber and Jelinek, 2006). It has been proposed that this strategy constrains the ability of howlers to adjust their behavior to changing socioecological factors (e.g., activity patterns: Bicca-Marques, 2003). Nevertheless, time-budgets and foraging behavior of howlers vary as a function of a number of social and ecological factors such as group size (e.g., Knopff and Pavelka, 2006), seasonal differences in the availability of plant parts (e.g., Chiarello, 1993; Estrada et al., 1999; Palacios and Rodriguez, 2001; Dunn et al., 2009) or habitat disturbance (e.g., Clarke et al., 2002; Behie and Pavelka, 2005; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Arroyo-Rodríguez and Dias, 2010).

The influence of reproductive state on female howlers' time-budgets and foraging has not been assessed to date, but the observed behavioral variation resulting from social and ecological factors suggests that females may be able to modify their behavior in order to meet the energetic demands of lactation. Therefore, although black howlers display an energy minimizing strategy, we predicted that time-budgets and foraging patterns should differ between lactating and nonlactating females and vary across females at different lactation stages. Specifically, we predicted that 1) lactating females should spend more time inactive and consume more high-quality foods than nonlactating females to compensate for increased energy expenditure during lactation; and 2) during early lactation, females should be more active and forage more intensively than in late lactation to adjust their metabolic balance to higher caring requirements of younger infants.

## METHODS

### Study site and subjects

The study was conducted between April 2005 and November 2008 in the Mexican state of Campeche, located in the Yucatan Peninsula. The climate is hot and humid (Vidal-Zepeda, 2005), and average annual rainfall is 1,300 mm, with a drier season from November to May (average monthly rainfall  $\pm$  SD =  $43.7 \pm 25.8$  mm), and a wetter period between June and October ( $218.9 \pm 14.1$  mm). The mean annual temperature is 26°C.

We studied 32 females and 35 infants belonging to 14 groups of black howlers that lived in different locations in this state (Table 1). Average ( $\pm$  SD) group size was  $6.14 \pm 2.25$  individuals, with  $1.79 \pm 0.7$  males,  $2.29 \pm 0.9$  females, and  $2.07 \pm 1.2$  immatures (i.e., individuals <30 months). The precise age of adult females could not be determined, but we selected full grown females for this study. Ages of 15 immatures were known, as they

TABLE 1. Size, composition, and geographic location of study groups

Site	Group size	Males	Females	Immatures	Latitude	Longitude
AA Álamo	4	1	2	1	18°48'45.44" N	90°58'54.61" W
Atascadero	4	2	1	1	18°42'35.59" N	90°53'32.44" W
Calakmul 9	5	2	2	1	18°27'49.89" N	89°53'57.24" W
Calakmul 27	9	3	2	4	18°19'0.28" N	89°51'28.92" W
Calaxchil	6	1	2	3	18°51'15.38" N	91°18'41.70" W
Chicbul	4	1	2	1	18°46'51.66" N	90°56'13.45" W
Chilar	8	2	3	3	18°54'6.58" N	90°53'37.90" W
Manantiales	3	1	1	1	18°42'55.39" N	91° 4'42.07" W
Oxcabal	5	2	2	1	18°51'44.34" N	90°57'39.45" W
R Álamo	8	1	4	3	18°48'42.15" N	90°58'58.69" W
Subestación	5	2	2	1	18°45'7.44" N	90°57'35.17" W
T61Calax	9	2	3	4	18°50'52.35" N	91°18'27.12" W
Tormento N	10	3	4	3	18°36'50.68" N	90°48'25.93" W
Tormento S	6	2	2	2	18°36'27.29" N	90°48'51.44" W

were born during our observations. The age of the remaining immatures was estimated based on the classification of Bolin (1981) and on our personal observations of infant development. Black howler immatures of more than 14-months old are rarely carried during locomotion and eat mainly solids when the group is foraging, with occasional suckling occurring only when the mother is resting. Therefore, for the purposes of the present study, we classified females as lactating (i.e., with infants of <15 months) or nonlactating (i.e., with no associated immatures or with immatures >14 months), and defined female lactation stage (FLS) as a function of the estimated age (in months) of infants associated with each female (i.e., FLS 1–14).

### Behavioral observations

We used focal-animal sampling with continuous recording (1-h samples; Altmann, 1974) to study time-budgets and foraging. We recorded time-budgets of adult females using EZrecord for Palm Pilot, and categorized behavioral observations into the following: feeding, resting, moving, social activity (i.e., affiliation, agonism, sexual behaviors, and vocalizing; excluding interactions with own offspring). During feeding we noted time dedicated to the consumption of leaves and fruits. Also, all trees used by the females were marked, numbered and located with a handheld global positioning system. Each marked tree that was used as a food source was identified to species level. Plants that could not be identified in the field were collected for identification at the "Alfredo Barrera Marín" (UADY) and UCAM (Centro de Investigaciones Históricas y Sociales, UAC) herbaria. Finally, all trees used by the focal females were digitized as points with ARC VIEW 3.2 (Environmental System Research Institute, USA), and ranging distances were calculated as the sum of the lengths (in meters) of straight lines connecting individual tree points used by females during each focal sample.

Observations were performed during complete days (i.e., 6:00–7:00 to 17:00–18:00, depending on the time of year), and all females were identified by their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers, and genital morphology and pigmentation. Focal females were selected on a pseudorandom basis: 1) we never collected two consecutive samples from the same female, and 2) during each observation day, priority was given to females that had been sampled infrequently.

This study was part of a broader project on the behavioral ecology of black howlers in Campeche, and our field work was based on following groups for about 130 h in each season (i.e., dry and wet seasons). Because of rotation of observations among study groups, sampling periods in each group were separated by at least 5 months. Each female was observed at least once in each season. When sampling periods extended for more than 1 month, females that had dependent infants were classified in two different FLS according to changes in infants' ages. We collected a total of 2,224 focal samples for lactating (1,840 h, 62 female periods) and nonlactating females (384 h, 29 female periods), with a mean ( $\pm$ SD) observation time of  $69.5 \pm 18.1$  h per female and a mean observation time of  $148.3 \pm 74.8$  h per FLS.

### Data organization and analyses

The presence/absence of lactating immatures (i.e., <15 months) was used as a categorical variable to compare time-budgets and foraging between lactating and nonlactating females, and FLS was used as a categorical predictor of differences in time-budgets and foraging across lactating females. Because of flooding of several study sites during the wet season, the majority of our samplings were performed in dry seasons (Table 2). This bias resulted in small sample sizes for several FLS in wet seasons (e.g., 1, 2, 9, and 10) and limited the possibility to compare female behavior across FLS according to seasonality. Therefore, we only analyze the effects of seasonality (as a categorical predictor, i.e., wet vs. dry) on female behavior in overall comparisons between lactating and nonlactating females.

The time each female spent in each time-budget component (i.e., feeding, resting, moving, and social activity) during focal samplings was transformed into percentage of activity, and time dedicated to feed from fruits and leaves were transformed into percentages of total feeding time per focal sample. The number of trees and plant species used by females as food sources were analyzed as frequencies per focal sample, and ranging distances were analyzed as the total distance covered by a female during each focal period.

To test for differences between lactating and nonlactating females in each of our time-budget (i.e., feeding, resting, moving, and social activity) and foraging variables (i.e., ranging distances, number of feeding trees, number of feeding species and proportion of time dedicated to feed from leaves and fruits), we used generalized linear mixed models that controlled for repeated measures of

TABLE 2. Total and seasonal sample sizes for FLS

	FLS														Total	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14		NL <sup>a</sup>
Wet	0	0	2	1	2	1	1	2	0	0	0	2	1	1	9	22
Dry	5	4	5	2	2	5	4	4	4	2	5	2	4	1	20	69
Total	5	4	7	3	4	6	5	6	4	2	5	4	5	2	29	91
Hours	147	148	252	112	105	113	147	136	124	121	110	105	111	109	384	2,224

<sup>a</sup> Nonlactating.

the same female in the same and different sampling periods as well as for the potential influence of seasonality. We also used analysis of deviance (ANODEV) to compare behavioral variables between baseline values (i.e., nonlactating females) and each FLS, followed by post hoc analyses with contrasts (Crawley, 1993). The ANODEV is a statistical test analogous to analysis of variance (ANOVA), but one that analyzes the structure of the error distribution with a link-function related to a specific distribution (e.g., Poisson, gamma, binomial). Data were corrected for overdispersion using the Pearson  $\chi^2$  estimate (Crawley, 1993). Note that females belonging to different groups were compared; however preliminary analyses indicated that group identity did not affect our results. Therefore, we did not include group as a predictive factor in our tests.

To identify general trends in the behavior of lactating females according to the age of their immatures, we first reduced the large set of time-budget and foraging variables to a smaller set of orthogonal factors using principal components analysis (PCA). A cluster analysis of the resulting components that had eigenvalues  $\geq 1$  was performed to identify similarities among females at different FLS, and the resulting clusters were then compared with one-way ANOVA.

For each dependent variable we report means  $\pm$  standard errors (SE). All tests were two-tailed and significance was set at  $\alpha = 0.05$ .

## RESULTS

### Time-budgets and ranging

Lactating females spent a higher proportion of their time resting ( $75.22\% \pm 0.74\%$  vs.  $68.66\% \pm 1.46\%$ ;  $\chi^2_1 = 37.590$ ,  $P < 0.001$ ), but less time feeding ( $14.24\% \pm 0.53\%$  vs.  $20.81\% \pm 0.98\%$ ;  $\chi^2_1 = 27.032$ ,  $P < 0.001$ ), moving ( $9.81\% \pm 0.38\%$  vs.  $13.13\% \pm 0.79\%$ ;  $\chi^2_1 = 50.469$ ,  $P < 0.001$ ) and in social activities ( $0.73\% \pm 0.12\%$  vs.  $5.96\% \pm 0.34\%$ ;  $\chi^2_1 = 5.498$ ,  $P = 0.019$ ) than nonlactating females. In all models, neither season nor the interaction between season and FLS were significant.

Figure 1 shows the observed and predicted activity times for each time-budget component according to FLS. There were significant differences between baseline values (nonlactating females) and FLS in feeding ( $\chi^2_{1,14} = 32.803$ ,  $P < 0.01$ ), resting ( $\chi^2_{1,14} = 30.994$ ,  $P < 0.01$ ), moving ( $\chi^2_{1,14} = 48.522$ ,  $P < 0.001$ ), and social activity ( $\chi^2_{1,14} = 30.868$ ,  $P < 0.01$ ). When compared to baseline values, feeding times were significantly higher for FLS 1, 2, and 9, and lower for FLS 3, 4, 7, 8, and  $>10$  (all contrasts  $P < 0.05$ ; Fig. 1a). Lactating females at FLS 3, 5, 7, and  $>10$  spent significantly more time resting than nonlactating females (all contrasts  $P < 0.05$ ; Fig. 1b). Females at FLS 4, 6, and 8 spent more time moving, but those at 1, 3, 5, 9, 10, and  $>11$  months moved less (all contrasts  $P < 0.05$ ; Fig. 1c). Finally, with the exception

of females at FLS 10, which spent more time in social activities, and females at FLS 1 and 13, which did not differ from baseline, females at all other FLS spent less time socializing with other adults than nonlactating females (all contrasts  $P < 0.05$ ; Fig. 1d).

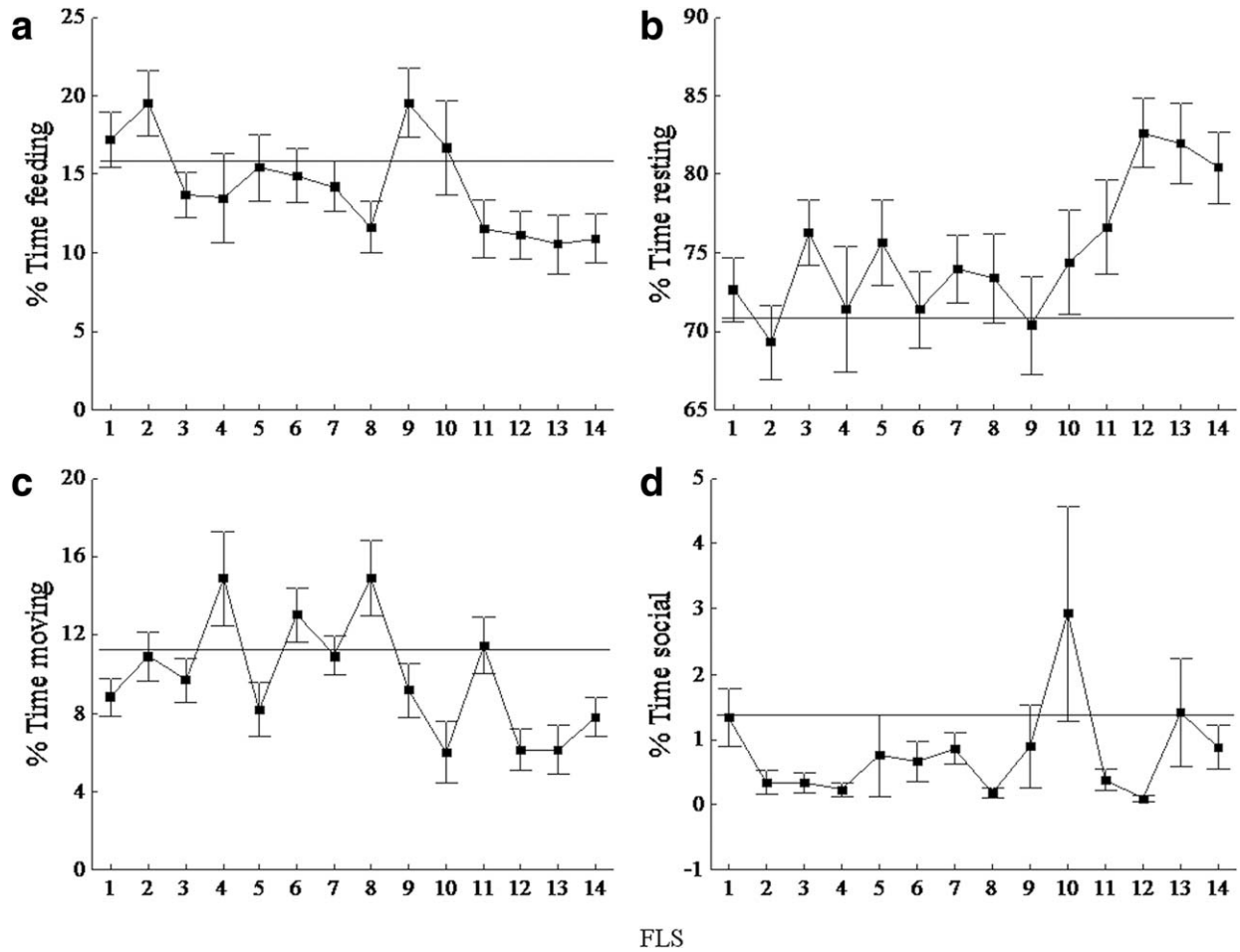
### Foraging patterns

Lactating ( $37.29 \pm 1.97$  m) and nonlactating ( $35.4 \pm 3.17$  m) females showed no differences in hourly ranging distances ( $\chi^2_1 = 0.238$ ,  $P = 0.626$ ), number of feeding trees used ( $0.8 \pm 0.03$  vs.  $0.92 \pm 0.07$ ;  $\chi^2_1 = 3.265$ ,  $P = 0.071$ ), number of feeding species used ( $0.83 \pm 0.04$  vs.  $0.94 \pm 0.07$ ;  $\chi^2_1 = 2.408$ ,  $P = 0.121$ ) and proportion of time dedicated to consuming leaves ( $44.13\% \pm 1.59\%$  vs.  $50.97\% \pm 2.81\%$ ;  $\chi^2_1 = 1.806$ ,  $P = 0.179$ ). However, lactating females fed for a significantly higher proportion of time from fruits ( $25.65\% \pm 1.37\%$  vs.  $16.41\% \pm 1.97\%$ ;  $\chi^2_1 = 16.778$ ,  $P < 0.001$ ). In all models, there was no significant effect of season or interaction between season and FLS.

The foraging patterns of lactating females differed from baseline levels at different stages (ranging:  $\chi^2_{1,14} = 79.719$ ,  $P < 0.001$ ; number of trees:  $\chi^2_{1,14} = 69.902$ ,  $P < 0.001$ ; number of species:  $\chi^2_{1,14} = 71.526$ ,  $P < 0.001$ ; time consuming leaves:  $\chi^2_{1,14} = 57.167$ ,  $P < 0.001$ ; time consuming fruits:  $\chi^2_{1,14} = 50.922$ ,  $P < 0.001$ ). First, females at FLS 1, 6, and 7 had longer ranging distances, whereas females at FLS 10, 13, and 14 had shorter ranges (all contrasts  $P < 0.05$ ; Fig. 2a). Second, females at FLS 10, 12, and 13 used significantly less trees (Fig. 2b) and less tree species (Fig. 2c) as food sources than nonlactating females (all contrasts  $P < 0.05$ ). Third, females at FLS 10-14 spent less time eating leaves (all contrasts  $P < 0.05$ ; Fig. 2d). Finally, females at FLS 2, 3, 6, 10, and 13 spent more time consuming fruits (all contrasts  $P < 0.05$ ; Fig. 2e).

### Trends in time-budgets and foraging according to FLS

A PCA of all time-budget and foraging variables resulted in two components with eigenvalues  $>1$ , which explained 80% of the total variance in those variables. Component 1 (eigenvalue = 6.13, % of variance = 58.8%) correlated strongly (i.e.,  $r > \pm 0.70$ ) and positively with time spent resting ( $r = 0.80$ ), and negatively with time spent moving ( $r = -0.82$ ), ranging distances ( $r = -0.77$ ), the number of feeding trees ( $r = -0.84$ ) and feeding species ( $r = -0.95$ ), and the proportion of time spent feeding from leaves ( $r = -0.88$ ). Component 2 (eigenvalue = 1.91, % of variance = 21.2%) correlated strongly with feeding ( $r = -0.84$ ) and social activity ( $r = -0.71$ ). Note that the proportion of time dedicated to consuming fruits had its highest factor score in a third component that had a low eigenvalue (0.92; % of variance = 9.3%). However, even in that component, it



**Fig. 1.** Time budgets (mean  $\pm$  SE) of female black howlers according to FLS: a) feeding; b) resting; c) moving; d) social activity. Solid lines represent baseline values of nonlactating females.

only reached a medium correlation coefficient ( $r = -0.60$ ). A cluster analysis relating each component with FLS separated lactating females into two groups: Component 1: FLS 1–10, FLS 11–14 (Fig. 3a); Component 2: FLS 1–9, FLS 10–14 (Fig. 3b).

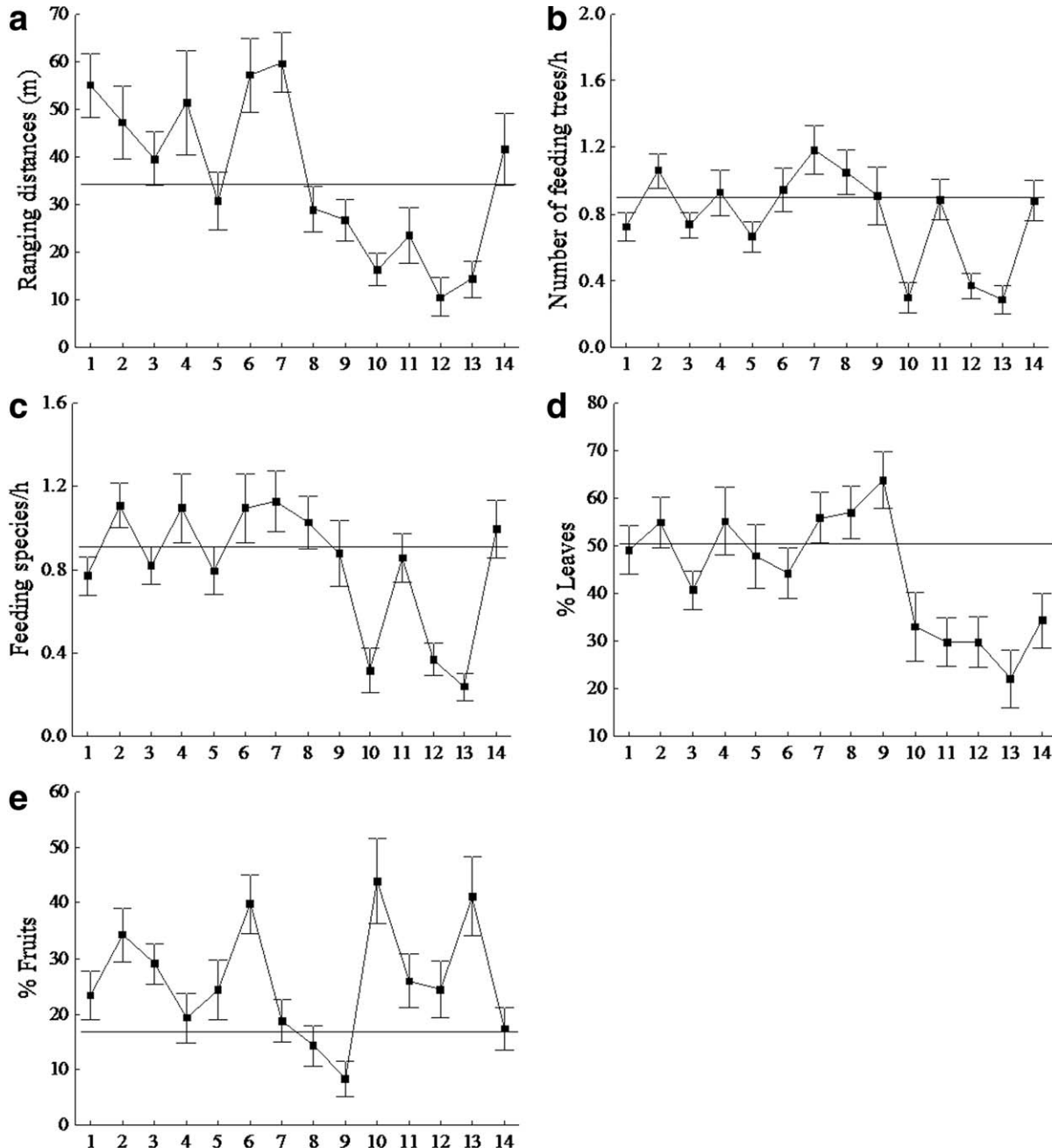
On the basis of this classification, we compared female component scores between the two groups in each component. The analysis of Component 1 indicated that, in contrast with females at FLS 11–14, females at FLS 1–10 spent less time feeding and in social activities ( $F_{1,12} = 6.320$ ,  $P = 0.027$ ) (Fig. 4b). Thus, females at FLS 1 to 9–10 rested less, feed more, devoted more time to social activities, moved more, ranged for larger distances, used more feeding trees and feeding species, and consumed more leaves. Females at FLS 10–11 to 14 showed the opposite pattern.

## DISCUSSION

As predicted, our analyses revealed that the time-budgets and foraging behavior of black howler females differ between lactating and nonlactating females, and across lactating females according to the age of their

immatures. Overall, lactating females spent more time inactive and feeding from fruits, but a complex picture emerged when comparing each FLS with baseline values, as for each analyzed variable at least three, usually nonconsecutive, FLS differed significantly from baseline values (i.e., nonlactating females). This picture was simplified through the reduction of variables and reclassification of FLS, which revealed that during the first two-thirds of lactation (i.e., females at FLS 1 to 9–10) females were more active (i.e., rested less, feed more, devoted more time to social activities and moved more) and foraged more intensively (i.e., ranged for larger distances, used more feeding trees and feeding species and consumed more leaves); the opposite trends were observed during the last third of lactation (i.e., females at FLS 10–11 to 14).

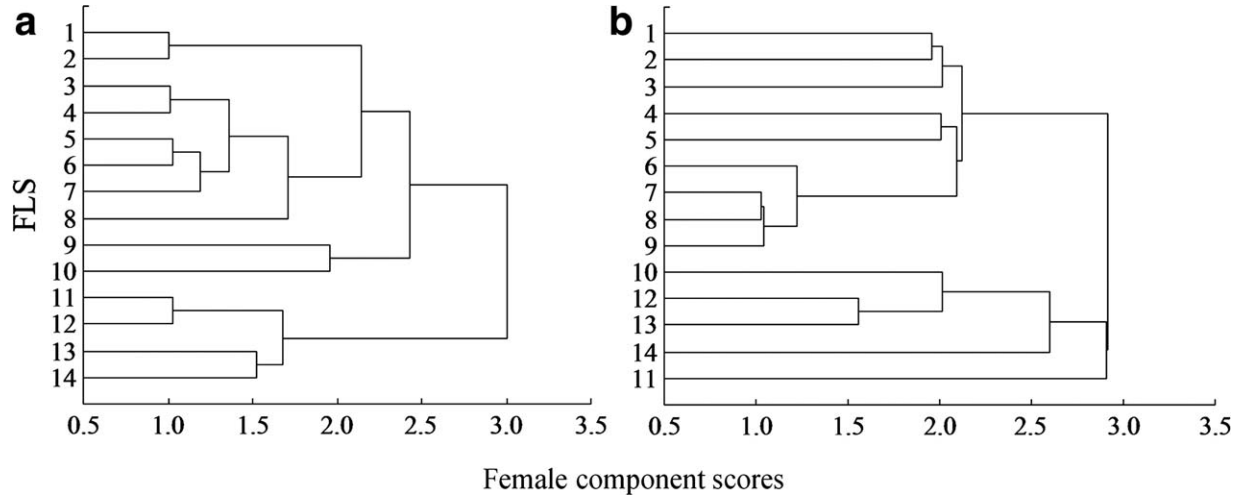
Our results suggest that, when compared to nonlactating females, lactating black howler females offset the energetic demands of lactation by decreasing activity and the consumption of high-quality foods (i.e., fruits). Howlers' time-budgets are very conservative as a result of their energy-saving adaptations to a highly folivorous diet and lack of digestive system specialized in the digestion of cellulose (Milton, 1980; Bicca-Marques, 2003). However, there is evidence that howlers adjust time-budgets to variation in food availability, and resting times in particular increase in response to temporal



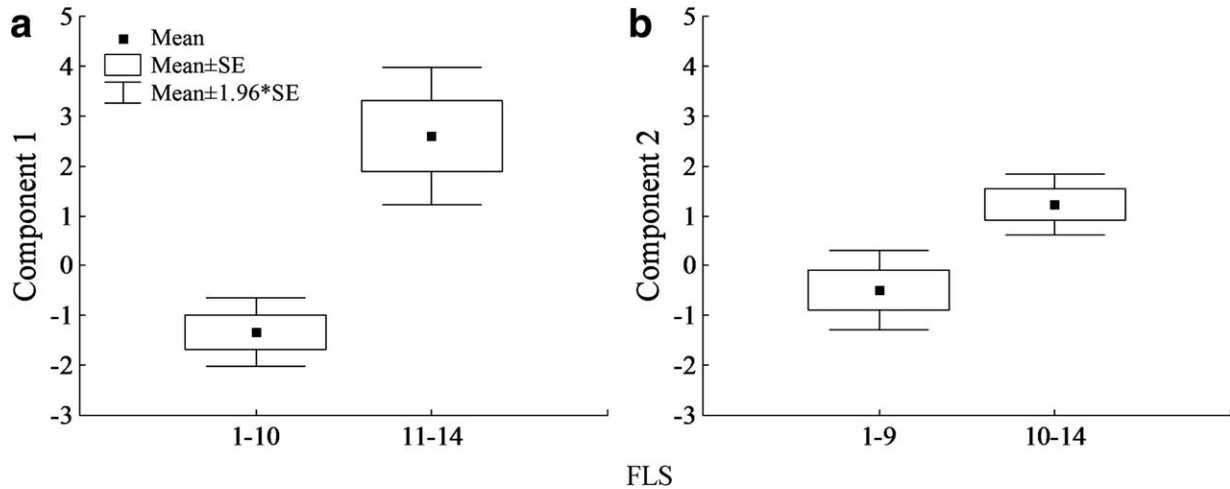
**Fig. 2.** Foraging behavior (mean  $\pm$  SE) of female black howlers according to FLS: **a**) ranging distances; **b**) number of feeding trees; **c**) number of feeding species; **d**) proportion of leaves in diet; **e**) proportion of fruits in diet. Solid lines represent baseline values of nonlactating females.

(Chiarello, 1993; Bravo and Sallénave, 2003) or spatial (Juan et al., 2000; Asensio et al., 2007) scarcity. Therefore, for female black howlers, resting time may be a store of uncommitted time that can be used during energy demanding reproductive states (Dunbar and Shannan, 1984). Higher inactivity by lactating females may also result from increases in time dedicated to vigilance. Although we did not study vigilance, there is consistent evidence suggesting that black howler females are more vigilant during lactation, probably as a result of infanticide risk (Treves et al., 2003; Kitchen, 2006). As vigilant females are usually stationary while scanning their surroundings (Treves et al., 2003), conspecific

threat may act as an additional constraint on the activity of lactating females, as has been observed in other primates (e.g., Barrett et al., 2006). Countering this possibility is the fact that time spent resting was higher during late lactation, when vulnerability to infanticide decreases in howlers (Crockett, 2003). Lactating females also increased the consumption of foods that are rich in ready energy (Milton, 1980), which may allow them to increase their caloric intake despite spending less time active. The fact that time dedicated to consume fruits did not load significantly in the PCA also suggests that lactating females relied heavily on this food item independently from their FLS. A similar pattern of reducing



**Fig. 3.** Dendrogram representing the results of the cluster analyses of the components obtained with the PCA of all time-budget and foraging variables: **a)** Component 1; **b)** Component 2.



**Fig. 4.** Comparisons between the groups of FLS defined through the cluster analysis: **a)** Component 1; **b)** Component 2.

activity (e.g., Harrison, 1983; Dunbar and Dunbar, 1988; Barrett et al., 2006) and consuming better quality foods (e.g., Boinski, 1988; Sauther, 1994; McCabe and Fedigan, 2007; Murray et al., 2009) during lactation has been observed in other primate species.

Concerning variation in female behavior throughout lactation, our analyses separated FLS into two groups. The first group included females in the first two-thirds of lactation, and was characterized by higher activity levels and more intensive foraging. In other primate species, females feed more during the early stages of lactation in order to compensate for a lower efficiency of lactation (cf. Blackburn and Calloway, 1976), and move more to maintain contact with infants (Altmann, 1980; Dunbar and Dunbar, 1988); this is therefore the period when females probably face the highest energetic demands (Crockett and Rudran, 1987). At this stage, females also consumed more leaves, which are usually richer in protein than fruits (Milton, 1980). The maximization of protein intake by lactating females has been observed in mantled howlers (*Alouatta palliata*: Serio-Silva et al., 1999) and other primate species (e.g., red titi

monkeys, *Callicebus cupreus*: Herrera and Heymann, 2004; vervets, *Chlorocebus aethiops*: Lee, 1987), and is consistent with the argument that lactating females have higher protein requirements associated with the production of milk (Widdowson, 1977; Sampson and Jansen, 1984). Finally, during the first two-thirds of lactation, females spent more time engaged in social activity. This concurs with the observations of Dunbar and Dunbar (1988), who found that geladas conserve time dedicated to social activity during most of the lactation period, with reduction of social time occurring during the later stages of lactation. Attraction toward newborns could explain increases in social activity during early lactation, as in many primate species group members crowd around new mothers (Maestripieri, 1994). However, our data suggest that differences between lactation stages were mainly determined by a four-fold increase in time spent in social activities by females with 10-month infants. The two females that we observed at this FLS copulated during sampling periods, so sexual activity, which included proceptive behaviors and consortship formation (Van Belle et al., 2009), explains why they had

such a pronounced increase in social activity. Considering the 15.5 month interbirth interval observed for black howlers in Campeche (Rangel-Negrín et al., 2009) and a gestation of 6 months (Van Belle et al., 2009), females with 10-month infants may be already cycling and reproducing again (Van Belle et al., 2009), so the peak in social activity associated with sexual behavior that we observed in this study may be recurrent among female black howlers at this FLS.

During the last third of lactation (i.e., females at FLS 10–11 to 14) females showed the highest levels of inactivity and foraged less intensively. This trend probably reflects the effects of two main factors, the increasing costs of caring for older infants and a new gestation. In contrast with infants older than 14 months, who are mostly independent, mantled howler infants with 8 or 9 through 13 or 14 months are still carried by the mother during locomotion and rely heavily on suckling (Balcells and Veà, 2009). Although no systematic comparative evidence exists for black howlers, our observations suggest a similar pattern for this species (Dias, personal observation). Therefore, we speculate that during late lactation the energetic demands of nursing are influenced by caring for heavier infants (Dunbar and Dunbar, 1988; Altmann and Samuels, 1992). As at this stage females also feed less than nonlactating females and females at early lactation, they are probably maximizing the trade-off of feeding time for resting in order to maintain their energetic balance. On the other hand, there is some evidence that females in this stage are already pregnant, as discussed above. In several primate species pregnant females face lower energetic constraints than lactating females, but still higher constraints than cycling females without infants (e.g., white-faced capuchins; McCabe and Fedigan, 2007; chimpanzees: Murray et al., 2009). Therefore, the combined effects of caring for older infants and pregnancy could force female black howlers to exacerbate the typical energy-saving strategy of howlers during late lactation (although this suggestion should be treated with caution, as we could only determine actual pregnancy in eight females).

There were no significant effects of seasonality on the behavioral differences observed between lactating and nonlactating females, a result that was probably determined by the fact that our observations were biased in favor of dry seasons. In primates, the timing of births is mostly determined by body condition, and as a consequence, is associated with food availability (Janson and Verdolin, 2005). Among black howlers there is a cluster of births during the dry season (Brockett et al., 2000), when fruit availability is probably lower (Valero and Byrne, 2007). Therefore, it would be expected that females in the same FLS but sampled in different seasons would present differences in their behavior as a consequence of fluctuations in the availability of food. A test of this prediction requires further research based on similar sampling efforts in both seasons of females at different FLS. We were also unable to perform an assessment of the energetic constraints of lactation on female time-budgets, as has been proposed by Altmann (1980). Estimations of body weights of neonates and growth rates of infants are essential parameters to test Altmann's model, but are currently unavailable for black howlers. Also related to the energetics of lactation, insight could be gained in future studies by gathering detailed data on the nutritional contents of foods consumed by lactating and nonlactating females.

In conclusion, the time-budgets and foraging behavior of black howlers differ between lactating and nonlactating females, and across lactation stages. Overall, lactation seems to force females to reduce activity and to maximize the intake of high-quality foods, with inactivity being the highest during late lactation, when females probably face the cumulative effects of nursing older infants and being pregnant. Early lactation, in contrast, is characterized by more activity and a higher consumption of protein-rich foods. Therefore, early lactation is probably the most energetically demanding stage of lactation. The time-budgets and foraging behavior of howlers have been extensively studied (Di Fiore and Campbell, 2007) and seem to be highly conservative across species (Bicca-Marques, 2003). This probably reflects phylogenetic constraints and convergence in foraging strategies across taxa. However, the present study demonstrates that reproductive state affects several dimensions of female behavior. It is therefore possible that variation in time-budgets and foraging strategies of howlers and other folivorous-frugivorous primates has been underestimated by previous research that has not assessed behavioral variation among females associated to physiological differences.

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