

Valerie A. Gann
Department of Anthropology
Southern Illinois University-Edwardsville

Sex Differences and Spatial Proximity on Feeding Behaviors in a Free-ranging Population of Mantled Howler Monkeys (*Alouatta palliata*) in northeastern Costa Rica

In general, primates are long lived and invest more time in the post-natal care of their young than do other mammals (Richard, 1985). This longer period of parental investment increases the females' cost in providing for infants but may play a major role in ensuring offspring survival. Studies on the cost of reproduction indicate that lactating females have higher nutritional requirements than both non-lactating females and adult males (Richard, 1985). Therefore, lactating females face certain feeding challenges in order to meet these metabolic needs. For instance, females may attempt to accommodate their increased nutritional requirements of reproduction by placing themselves in close proximity to the adult males during feeding in order to obtain access to productive feeding sites (Richard, 1985). Females may also space themselves near vigilant adult males in an attempt to avoid infanticide by invading males.

Given these two alternative spacing strategies, three important questions can be addressed: (1) Are there sex differences in feeding behavior, diet, traveling and resting in mantled howler (*Alouatta palliata*) monkeys? (2) Do certain sex classes maintain proximity to other sex classes more frequently than expected by chance and if so, does this change during different activities? (3) If males have priority access to productive feeding sites, do females avoid feeding near adult males due to male aggressiveness or do they maintain proximity to males in order to obtain access to better feeding opportunities and protection for their young? These questions were examined during a field study of a free-ranging population of mantled howlers (*Alouatta palliata*). The study compared the distances that lactating females and non-lactating females/subadult males maintained from adult males during feeding, foraging, traveling and resting.

Methods

The present paper examines the spatial proximity between sex classes of a group of free-ranging mantled howler monkeys (*Alouatta palliata*) at the La Suerte Biological Field Station in Northeastern Costa Rica. The period of investigation extended from January 9, through January 13, 1997. The locality is characterized by an average rainfall is 3800 mm (150 inches) with an altitude of 50 m above sea level. The field station maintains 700 acres (283.4 ha) of advanced secondary forests, swamps and pastures. Most of the

property lies along the Rio Suerte, which is a river that empties into the Caribbean at Tortuguero National Park.

Methods of observation consisted of two minute focal animal sampling using two minute intervals (Altmann, 1974; Dunbar, 1976). Individuals were divided into four sex class categories: adult males, adult females without infants/subadult males, adult females with infants and unknown. Infants and juveniles were not included in the observations. Observations recorded time spent feeding, foraging, traveling and resting within all three sex-classes. When the focal animal was lost from view, the next visible animal became the new focal animal.

A total of 504 2-minute individual activity records or 16.8 hours of observation recorded for *Alouatta palliata*. Quantitative information presented herein was obtained from 6 days of observation during a primate ecology field school. A small group of 8 howler monkeys were followed between the hours of 0500 to 1150 and from 1250 to 1600. A total of 64 hours were spent in the field. Observation hours were limited due to dense canopy and the lack of characteristic dawn calls normally displayed by this species. Feeding activities were defined as handling of food items and ingestion. Time spent resting was defined as a period of inactivity. Travel was defined as movement through the canopy and crossing between gaps. Foraging was defined as movement in the crown of a feeding site and visual scanning in search of food. Proximity to the focal animal was measured using the metric distance of the nearest neighbor according to the following ordinal scale: 1. Touching = 0 meters; 2. > 0 < 1m; 3. 1 - 2m; 4. 2 - 3m; 5. 3 - 5m; 6. 5 - 10m; 7. > 10m

Results

Overall Activity Budgets

Results of activity budgets of *Alouatta palliata* at La Suerte are similar to those found at other study sites. Overall the results indicate that *A. palliata* spent a majority of their daily activity time at rest (64.8%) (Table 1). Although other studies have combined

Table 1. Average time in percent spent on daily activities.

Activity	Male		Female N		Females L		Overall(n)		
	%	n	%	n	%	n	%	n	
Feeding	9.0	14	20.0	25	18.0	40	16.46	79	
Traveling	19.0	29	10.4	13	18.0	41	15.67	83	
Resting	71.0	111	60.8	76	62.5	140	64.80	327	
Foraging	1.0	1	8.8	11	1.3	3	2.9	15	
Overall Total								504	

*N= non-lactating female, L = lactating female

their feeding and foraging into a single category, in this study these activities were recorded separately. Data were also collected on activity budgets within each sex class. The results indicated that howlers spent an average of 15.67% of their time traveling between feeding and resting sites (Table 1.).

Comparison of Foraging Behaviors Within Sex Classes

Although overall results of within group activity patterns were similar to other studies, marked differences between lactating and non-lactating females/subadult males were observed. Non-lactating females spent an average of 8.8% of their time foraging while lactating females spent 1.3% of their time foraging. Differences in time spent foraging may be explained by the lactating females ability to obtain better access to productive food sites. In contrast, percentages of feeding times between lactating and non-lactating females did not differ (20% vs. 18%).

Proximity Differences Between Sex Classes

Spatial relationships between members of a social group offer insight into social bonds. The results of this study indicate differences in the distance that lactating females spent near to the adult male during various activities. Differences also existed in proximity to the adult male between the lactating and non-lactating females/subadult males. The lactating female maintained a distance of 1 to 3 meters to the male during times of feeding (figure 1).

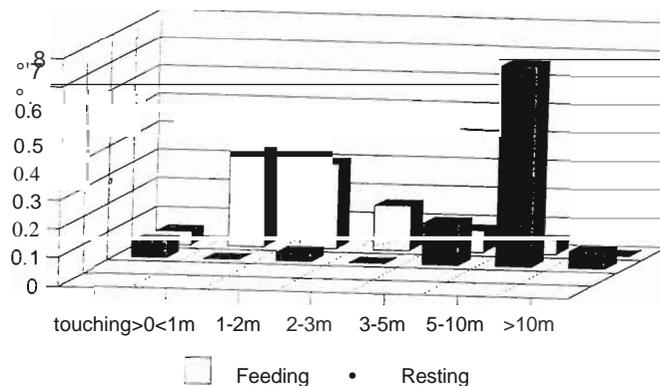


Figure 1. Distribution of nearest neighbor during feeding and rest. Focal animal is female with infant and nearest neighbor is male.

During times of rest, however, this female was a distance of 10 meters 70% of the time. The non-lactating female maintained closer distances to the male during times of rest, (within 1-3 meters) than did the lactating female (Figure 2). Due to the problems of visibility and individual identification, no data was collected when the male was nearest neighbor to the non-lactating female during feeding. Therefore, a comparison of feeding behaviors between the non-lactating females and lactating females could not be examined.

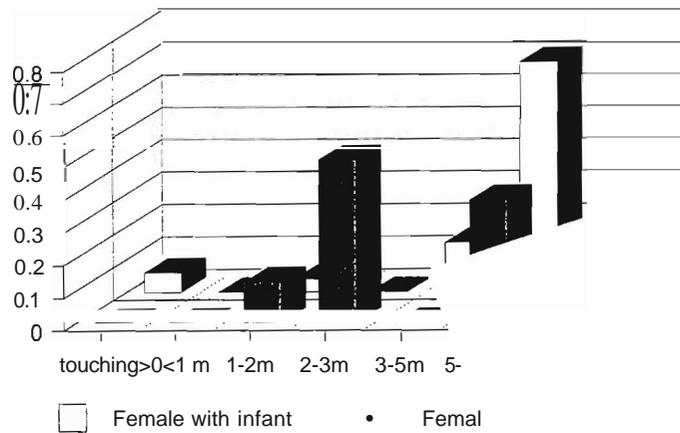


Figure 2. Distribution of nearest neighbor during rest. Focal animal is female without infant and female with infant. Nearest neighbor is male.

Comparison of Feeding Behaviors Between Sex Classes

On the average, males spent less time feeding than lactating females. Males spent 9% of total activity time feeding. Lactating females spent 18% of total time feeding and non-lactating females 20%. Overall, adult females spent more time feeding than adult males, however, it is not possible to determine if this represents increased feeding time or decreased access to productive feeding sites.

Discussion

Data presented in this study indicated marked differences in time spent feeding and foraging between male and female mantled howler monkeys (*Alouatta palliata*) at La Suerte. Males spent 50% less time feeding and foraging than females (Table 1). This is contrary to

the prediction that males would spend more time feeding due to their large body size. In the species *Alouatta palliata*, males weigh 2 kg. more than females and may be expected to need more food to supply their nutritional requirements (Crockett and Eisenberg in Primate Societies, 1985).

In a study on Rhesus macaques (*Macaca mulatta*) (Ciani and Chiarelli, 1988) sharp differences in feeding strategies were reported between age and sex classes. In this particular study, males that fed in town reduced their feeding time more than any other age/sex class, even during the mating season (Ciani and Chiarelli, 1988). These differences were attributed to males preferring to feed in town by begging and stealing from their human neighbors, while females fed exclusively on resources found in the forest (Ciani and Chiarelli, 1988). In this study, reduced feeding time may be indicative of increased feeding rates (Ciani and Chiarelli, 1988). Larger adult male body size and increased aggression may have determined these different strategies of food selection.

From the results of the present study it can be suggested that adult male howlers may spend less time feeding than the time spent by females. This is possibly a result of better access to productive food resources. Recent studies of social behavior in *Alouatta palliata* have reported that based on aggressive interactions, adult males ranked above adult females (Jones, 1980). Therefore, access to food resources may be related to social rank with higher ranking animals having preferential access. In addition, males spent 10% more time resting and traveling than females. The increased time spent resting may have allowed adult males to offset costs associated with additional time spent traveling relative to the females.

This study also indicates that while there were differences in the activity budgets between sex classes, overall this group of mantled howlers exhibited similar activity budgets to other studied groups of *Alouatta palliata* (Milton, 1980, 1981; Glander, 1975) (see table 2). Proximity or distances between two individuals has been used as an index of the strength of the "bond" between individuals (Dunbar, 1976). Furthermore, sex and proximity of the nearest neighbor may have an affect on the focal animals food choice or foraging activities. This study focused on proximal distances of lactating and non-lactating females to the adult male during all activities. The lactating female maintained a proximal distance of 1-3 meters to the adult male during feeding.

Table 2. Percent time spent on principal activities at three study sites.

<u>Activity</u>	<u>Barro Colorado¹</u>	<u>Guanacoste²</u>	<u>La Suerte</u>
Feeding	16.24	18.08	19.36
Traveling	10.23	11.00	15.67
<u>Resting</u>	<u>65.54</u>	<u>65.30</u>	<u>64.80</u>

1. Milton 1985; 2. Glander 1975, cited in Milton 1985.

Note: Activity data Barro Colorado and Guanacoste are over an annual cycle. Data from La Suerte are from a six consecutive day period.

Previous studies have focused on relationships between feeding behavior, ranging patterns, inter-group spacing and ecology in primates (post, 1980; et. al.). In general, these studies

have examined ecological constraints of group size such as the abundance, density and distribution of food sources. These constraints may be most severe during times of food scarcity. For example, in a study on Chacma baboons (*Papio ursinus*) within-group competition over limited resources can result in severe loss of body weight and death for adult females and infants (Hamilton, 1985 in Garber, 1987). This would suggest that adult and sub-adult males prevented females from access to quality food sites (Garber, 1987).

Access to quality food sites may be particularly important for lactating females. For instance, during gestation, nutritional requirements increase by 25%, while lactation may increase needs by 50% (Richard, 1985). Maternal feeding behavior may affect mortality since the production of an ample supply of milk is dependent on the mothers ability to obtain sufficient food to supply herself and her growing offspring (Richard, 1985). According to Altmann (1977 in Richard, 1985), reduced milk production due to maternal nutritional stress is a major factor contributing to infant deaths in *Papio cynocephalus* (Altmann, 1977 in Richard, 1985).

Females may attempt to accommodate their increased nutritional requirements of reproduction by placing themselves in close proximity to the adult male in order to obtain access to productive feeding sites. These data suggest that lactating female howlers may have developed this behavioral feeding strategy in order to meet the increased nutritional requirements experienced during lactation and thus improve the chances of survivorship for their offspring.

Social factors may also influence infant mortality. In species such as *Gorilla gorilla*, Hanuman langurs and Red and Mantled howlers, male-male competition and reproductive strategies may result in infant deaths when extra group males take over a group and usurp the sovereign males breeding position (Richard, 1985). However, if females with infants are susceptible to acts of infanticide, then it would be expected that proximity to males would be consistently close during all activities.

These data suggest that non-lactating females maintained closer proximity (1-3 meters) to the adult male during times of rest than did lactating females (>10 meters) (see figure 1). As a result, these data do not support the idea that lactating females maintain closer proximity to vigilant adult males for protection from infanticide. If females with infants are susceptible to acts of infanticide, then proximity to males would likely have been similar during all activities.

Lactating females have higher costs associated with reproduction, however, non-lactating females are assumed to have the same energetic costs and nutritional needs as sub-adult males due to similarity of body weights. It has been suggested that lactating females should spend more time foraging than non-lactating females due to costs associated with lactation and caring for infants (Richard, 1985). However, these data show that non-lactating females spent 8.8% of daily activity time foraging while lactating females spent 1.3%. Non-lactating females may have to spend more time foraging than lactating females because lactating females may have had better access to productive feeding sites as a result of maintaining closer distances to the adult male during feeding.

Study Limitations

The sample size and time spent in field observation is relatively small compared to other studies. Problems were encountered in identifying sex of nearest neighbor, especially during times of rest high in the canopy. Future studies should include a group of marked individuals for ease in observations, data collection and identification of individuals. In addition, position within the crown of the focal animal and nearest neighbor, and nutritional analysis of foods selected may allow a better examination of specific differences on feeding behaviors between and within sex classes during all activities.

Conclusions

Non-lactating females spent a larger percentage of their daily activity foraging than non-lactating females. Males spent less time feeding and more time traveling and resting than females. Lactating females were in closer proximity to the male during times of feeding than non-lactating females. Non-lactating females were in closer proximity to the male than lactating females during times of rest. And finally, overall group activity budget results were similar to other studies on *Alouatta palliata*.

References Cited

- Altmann, J.
1974 Observational Study of Behavior: Sampling Methods. *Behaviour* 49:227-267
- Ciani, c.A., and Chiarelli, B.
1988 Age and Sex differences in the Feeding Strategies of a Free-Ranging Population of *Macaca mulatta* Zinunerman, 1788 (Primate Cercopithecidae), in Simla (India). *Monitore Zooligica Italiano* 22: 171-182.
- Dunbar, R.I.M.
1976 Some Aspects of Research Design and Their Implications in the Observational Study of Behaviour. *Behaviour* 58:78-98.
- Garber, P.A.
1987 Seasonal Patterns of Diet and Ranging in Two Species of Tamarin Monkeys: Stability versus Variability. *International Journal of Primatology* 14:145-166
- Glander, K.E.
1978 Habitat and Resource Utilization: An ecological view of Social Organization in Mantled Howler Monkeys. Ph.D. Dissertation, University of Chicago, Chicago.
- Jones, C.B.
1980 The Functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous Neotropical primate. *Primates* 21: 389-405.

- Milton, K.
1980 The Foraging Strategy of Howler Monkeys: A study in Primate Economics. New York: Columbia University Press.
- 1981 Food Choice and Digestive Strategies of Two Sympatric Primate Species. The American Naturalist 117:496-505.
- Post, D.H.M.
1980 Feeding Behavior of Yellow Baboons (*Papio cynocephalus*): Relationship to Age, Gender, and Dominance Rank. Folia Primatologica 34:170-195.
- Richard, A.F.
1985 Primates in Nature. New York: W.H. Freeman and Company.
- Slobodkin, I. B., and A. Rapoport.
1974 An Optimal Strategy of Evolution. Q. Rev. Biol. 49:181-200

Note: The author to acknowledge Greg Weston and Jill Pruett for their assistance in helping locate a group of howlers that seldom performed their characteristic dawn calls. The author also thanks Dr. David Bergeson, Barth Wright and Jennifer Rehg for their assistance and helpful comments on the manuscript. A special thanks is awarded Dr. Paul Garber for his guidance and encouragement, and to Wanda Strohkirch, Glenn Gann, Cody Foltz and Kenny G. for their caring support.