

## RESEARCH ARTICLE

# Female Dominance and Feeding Priority in a Prosimian Primate: Experimental Manipulation of Feeding Competition

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Female dominance and feeding priority are considered unique behavioral strategies in many Malagasy lemuriformes, particularly *Lemur catta*. Two hypotheses have been introduced to explain these behavior patterns: 1) females are agonistically dominant over males to mitigate female–male food competition so that females can compensate for high energy demands and inefficient reproductive physiology, and 2) males defer to females when feeding as a reproductive strategy. We tested these hypotheses by conducting controlled feeding experiments on free-ranging ring-tailed lemurs (*Lemur catta*) on St. Catherine’s Island, GA. Food was dispersed in three ways to simulate varying patch sizes. All feeding and agonistic interactions were recorded during each trial (n = 24). The degree of relatedness between individuals was determined using DNA fingerprinting. There was a clear relationship between food dispersion and both expression of female dominance and feeding priority. Elements of both hypotheses were supported because male and female *L. catta* used different strategies depending on rank and the dispersion of food. Interpretation of the impact of male rank was complicated because the younger, low-ranking males had female relatives in the group. Females fed more than males, and rates of aggression decreased as food dispersion increased. High-ranking, older unrelated males deferred to females and received little aggression. The top-ranking male deferred the most and sired most if not all of the offspring. Low-ranking, younger related males fought with females for access to food sources, received more aggression,

Contract grant sponsor: American Museum of Natural History; Contract grant sponsor: Duke University Research Council.

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Received 14 January 2006; revised 17 April 2006; revision accepted 25 April 2006

DOI 10.1002/ajp.20346

Published online 11 December 2006 in Wiley InterScience (www.interscience.wiley.com).

and did not sire offspring. *Am. J. Primatol.* 69:295–304, 2007. © 2006 Wiley-Liss, Inc.

**Key words:** lemurs; agonistic behavior; male deference; *Lemur catta*; female dominance; feeding priority

## INTRODUCTION

Female dominance is a social trait that has long been associated with many of the lemurs of Madagascar [Charles-Dominique & Petter, 1980; Gould et al., 2003; Jolly, 1966; Pereira et al., 1990; Perret, 1982; Pollock, 1979; Richard & Heimbuch, 1975; Sauther et al., 1999]. The ability of female lemurs to displace and elicit submissive behavior from adult males is especially significant given the rarity of such behavior among mammalian taxa. However, questions regarding the evolutionary basis of female dominance remain largely unresolved despite the growing body of research on lemur behavioral ecology.

One critical issue that has been examined is whether female dominance should be considered separately from female feeding priority [Jolly, 1984; Kappeler, 1990; Sauther, 1993]. Several authors have suggested that female feeding priority may not be possible without female dominance [Pereira et al., 1990]. In contrast, authors have also questioned the pervasiveness of female dominance among lemurs, and have suggested that in many of the so-called female dominant species, females may have priority of access to food resources but are unable to displace males in other contexts [Kappeler, 1990; Pereira et al., 1990]. Therefore, female feeding priority may be mediated primarily by male deference rather than by a female's ability to assert dominance over a male. These two perspectives on the evolution of female dominance and feeding priority in lemurs were previously summarized under two hypotheses, but whether these two hypotheses are mutually exclusive has yet to be tested in a controlled environment.

The first hypothesis is based on evidence that female lemurs face unusually high levels of physiological stress during reproduction [Young et al., 1990]. It has been argued that a combination of low basal metabolic rate, high degree of prenatal investment, altricial offspring, and rapid neonatal growth rate has shaped the evolution of female dominance so that group-living females can minimize energy expended during resource competition with males [Jolly, 1984; Richard & Nicoll, 1987; Sauther, 1993]. According to this hypothesis, female feeding priority is maintained by female dominance to maximize each female's reproductive success. If female dominance hierarchies influence feeding priority, then the following patterns should be observed: 1) female dominance rank should be positively correlated with intra- and intersexual feeding success, 2) higher-ranking females should feed more than low-ranking females and all males, and 3) males that are aggressed against the most should feed less.

Regarding the second hypothesis, it has been suggested that female feeding priority may have evolved via sexual selection if females selectively mate with males that display deferential behavior in feeding contexts [Hrdy, 1981; Kappeler, 1990; Pereira et al., 1990]. Therefore, males may be deferential to females in feeding contexts as a reproductive strategy. Deference in this context is defined as a male not attempting to feed when there is no aggressive exclusion from feeding by the female. If female feeding priority results from male deference, then one or more of the following patterns should be observed: 1) female feeding success should occur in the absence of agonistic interactions with males, 2) deferential

males should have greater mating success, and 3) females should direct more aggression toward nondeferential males.

To test these two hypotheses and their subsequent predictions, we conducted a series of experimental feeding trials using a social group of free-ranging ring-tailed lemurs (*Lemur catta*), a species in which female feeding priority and female dominance have been studied extensively [Jolly, 1966; Sauther, 1993; Sussman, 1974, 1977a, b]. *L. catta* is a diurnal, monomorphic, medium-sized (2–3 kg) species that lives in multi-male, multi-female troops of up to 24 individuals. Both sexes display linear dominance hierarchies. Females are philopatric and form one or more matrilineal groups that function as the social core of the group. By examining between- and within-sex dominance relations in *L. catta* during feeding, we can determine whether males and females of different ranks use different behavioral strategies to maintain feeding success.

## MATERIALS AND METHODS

### Study Site and Subjects

The study group of ring-tailed lemurs is free-ranging on the barrier island of St. Catherine's, located off the coast of Georgia. St. Catherine's Island covers approximately 57.8 km<sup>2</sup> and has several distinct habitats: mixed deciduous and evergreen forests, palmetto, savanna, and both fresh- and saltwater marshes [Thomas, 1988]. Several indigenous and introduced mammalian species live on the island, including ruffed lemurs (*Varecia variegata variegata*). One group of ring-tailed lemurs was released on St. Catherine's in 1984 and now there are currently four *L. catta* social groups on the island. The group used in this study ranged on the northern end of St. Catherine's where they were first released. The ring-tailed lemurs in the study group could be distinguished by unique collars and tags, and all of the lemurs were habituated to observers. Fresh fruit and commercial monkey chow were provided on a daily basis.

At the time of this study, the group consisted of nine adult individuals and two infants. There were four females: sisters LIB (7 years old) and GWI (5 years old); LIB's 2-year-old daughter, HEP; and NEW (3 years old), from a different but related matriline. Both LIB and NEW had infants at the time of the study. The five males included two 7-year-old unrelated adults (MCQ and OSS) and three natal males. The natal males (SIM and GEN, NEW's nephews; and KIL, LIB and GWI's nephew) were all 2-year-olds. SIM, GEN, and KIL's mothers were no longer in the group.

We determined individual dominance rank by examining unambiguous, decided interactions between dyads that involved the winner giving either aggressive (A) or no (0) behavioral signals, and the loser giving only submissive (S) signals [Pereira et al., 1990]. Individuals that consistently received submissive signals from other group members but rarely reacted submissively were considered dominant. Based on won agonistic interactions, the dominance rank of the females was GWI > NEW > LIB > HEP, and the dominance rank of the males was MCQ > OSS > GEN > KIL > SIM.

### Feeding Trials

We created food patches at the lemurs' usual provisioning site by scattering a mixture of chow and fruit in a circular area to simulate a two-dimensional food patch. Three circular areas of 1-m, 2-m, and 4-m radii were used. It is assumed that food distributed in circles with smaller radii (1 m and 2 m) can be more easily

monopolized by individuals than food distributed in circles with a 4-m radius. The amount of food distributed was equivalent at all radii lengths. The smallest of these patches were probably smaller than those typically experienced by wild *L. catta*. The medium and largest experimental patch sizes may be equivalent to patches encountered in the wild. Sussman [1974, 1977a] reported for *L. catta* in two study areas that 5-min feeding records differed in the size of the food sources used. At Antserananomby, approximately 44% of total records were obtained in large and medium trees (as defined by Sussman [1972]) and 45% were obtained in small trees, vines, and ground plants, whereas at Berenty the percentages for these categories were approximately 23% and 70%, respectively. However, all of the experimental patches probably contained more nutrition than would be typically found in a wild food source, since each experimental presentation contained an adequate diet for the study group for the day.

Approximately equal numbers of trials were conducted at each of the three radius lengths, for a total of 24 feeding trials (1-m radius  $n = 7$ , 2-m radius  $n = 9$ , 4-m radius  $n = 8$ ). The results from two additional trials were excluded from the analysis due to interference by other species (ruffed lemurs (*Varecia variegata*) and white-tailed deer (*Odocoileus virginianus*)) or the absence of some group members at the start of the feeding bout. To minimize the possibility of subject conditioning, only one trial was conducted each day and radius length was changed daily so that the same radius length was never duplicated on consecutive days. Trials were conducted between 15 May and 31 July 1994.

Data recording began when all of the food had been distributed and the first subject began to eat (designated as time 0). From time 0, the identity of all individuals feeding was recorded at 30-sec intervals until all group members had stopped feeding. Feeding priority in this study was inferred by differences between individuals in the proportion of sampling intervals spent feeding. In addition, all occurrences of agonistic interactions were recorded from time 0 until the end of the group's feeding bout [Altmann, 1974; Martin & Bateson, 1993]. The initiator, winner, loser, and length (if  $> 5$  sec) of the interaction were also recorded during food trials. Interindividual agonism was defined following Jolly [1966].

### DNA fingerprinting

The paternity of infants sired in the group in the October 1994 mating season following data collection was determined by DNA fingerprinting [Jeffreys et al., 1985a, b; Pereira & Weiss, 1991; Weiss et al., 1988]. DNA was extracted from white blood cells, digested, and hybridized with the probe 33.15 following published protocols for this species [Pereira & Weiss, 1991]. The DNA fingerprints of each offspring were compared with those of the mother and all males to identify potential fathers.

### Data Analysis and Statistics

Only data collected during the first 10 min of each feeding trial were used for analysis. The proportion of the 20 30-sec time points that was spent feeding was arcsine-transformed to fit analysis of variance (ANOVA) assumptions as far as possible [Sokal & Rohlf, 1995]. Within some of the feeding trials, some subjects ( $n = 8$  trials) fed for all or none of the time points in some trials, and the data could not be transformed to normality. However, these untransformed data were included in the analysis because ANOVA tests are robust to deviations from normality. Nonparametric rank correlations were used to compare the relationship between agonistic behaviors during feeding and each individual's rank.

**RESULTS**

Sex, dominance rank, and the size of the simulated food patch affected individual feeding success (proportion of 30-sec intervals spent feeding during the first 10 min of the feeding bout). On average, females fed significantly more than males at all three radius lengths (total feeding time points:  $n = 683$  for 1-m, 1,047 for 2-m, and 1,188 for 4-m radii; Table I). Sex differences in feeding decreased, however, with increasing radius length (Fig. 1). Individuals differed in their feeding success, and feeding success differed with the radius of the food trial, but there was no significant individual  $\times$  radius interaction (Table II). Male dominance rank was correlated with feeding success (i.e., the high-ranking male fed less than low-ranking males; Fig. 1). Female dominance rank, however, did

**TABLE I. Mean Number of 30-sec Time Points Spent Feeding During the First 10 min of the Feeding Bout\***

	Mean female	SE	Mean male	SE	F	P
1-m radius	17.21	0.67	5.74	1.00	93.73	0.0001
2-m radius	16.42	4.53	10.13	7.39	19.84	0.0001
4-m radius	18.25	2.14	15.10	5.63	8.49	0.0048

\*ANOVA computed on transformed data (see Materials and Methods).  
SE, standard error.

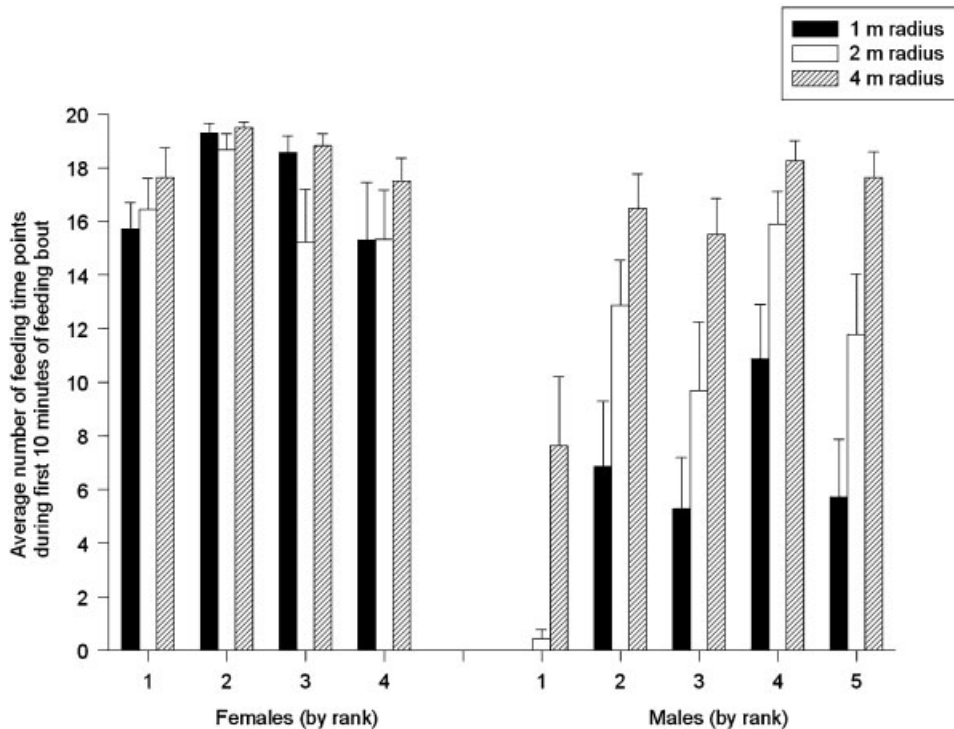


Fig. 1. Mean and SE number of 30-sec feeding time points during the first 10 min of each feeding bout.

**TABLE II. Results of the Two-Way ANOVA of Feeding Time With Radius and Individuals**

	Male		Female	
	F	P	F	P
Radius	1.61	0.2054	31.64	0.0001
Individual	4.56	0.0052	15.85	0.0001
Radius*individual	0.61	0.7190	0.59	0.7814

**TABLE III. Spearman Rank Correlation Coefficient of Intrasexual Dominance Rank and Feeding Success**

	1-m radius	P	2-m radius	P	4-m radius	P
Males	0.440	0.008	0.512	0.000	0.475	0.002
Females	0.076	0.698	-0.117	0.497	-0.164	0.369

not influence female feeding success (Table III). The amount of agonism directed by females toward males decreased with increased radius length ( $n = 473$  total agonistic interactions during feeding trials; Fig. 2). In the 1-m and 2-m radius length feeding trials, aggression received by males from females was correlated with male rank, with lower-ranking males receiving more aggression than higher-ranking males (Table IV). During feeding the females gave either aggressive or no signals, whereas the males gave only submissive signals. There was no significant correlation in the 4-m radius trials. Agonistic interactions were directed toward males by all females (Fig. 3).

DNA fingerprinting was carried out on four offspring: twins born to LIB, and singletons born to NEW and HEP. In the 1995 birth season the alpha male (MCQ) was the clear father of two and the probable father of the other two offspring.

## DISCUSSION

The predictions from both hypotheses regarding the evolution of female dominance were supported in this study. *L. catta* females were clearly female-dominant in that they consistently received submissive signals from males and directed aggression most often toward males, particularly low-ranking males in feeding contexts. In addition, female *L. catta* clearly had feeding priority in that they fed during a higher proportion of 30-sec time points than males. Female rank, however, did not influence female feeding success, since all females had approximately the same feeding time points.

Males of different ranks appeared to use different behavioral strategies when feeding. In this study, the alpha male never fed in the 1-m and 2-m food patches. In addition, the two top-ranking males were involved in significantly fewer agonistic interactions with group females than the lower-ranking males at all radii lengths. This suggests that females may in part maintain feeding priority in small food patches due to male deference from high-ranking males, as proposed in hypothesis 2. The highest-ranking, deferent male in this study also had higher reproductive success than the other males.

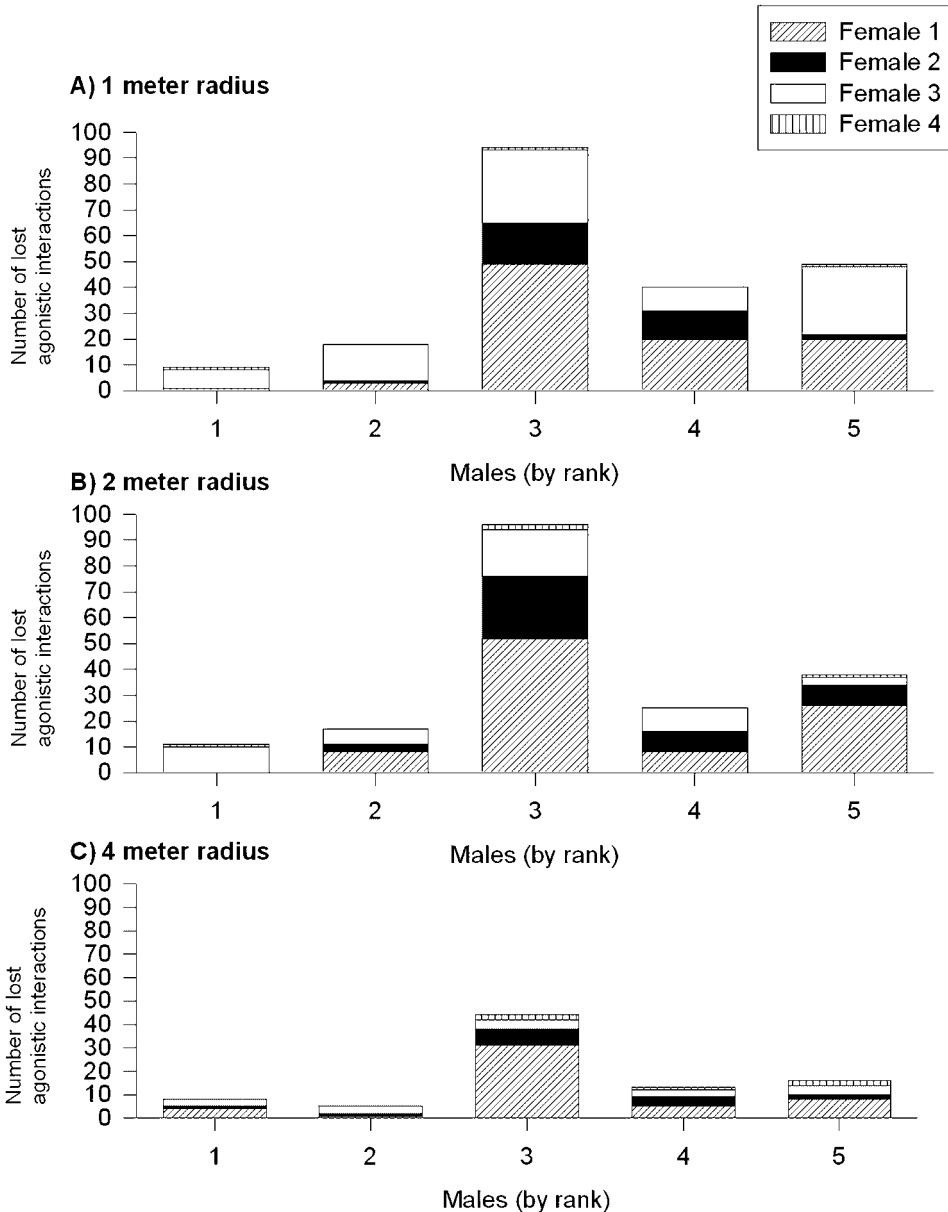


Fig. 2. Mean frequency and SE of submissive signals (S) given by males to female aggressive (A) or no (0) signals. Females are shown by order of rank.

The low-ranking males, in contrast, did not defer to females and received more aggression from females (hypothesis 2, prediction 3). These low-ranking males also fed less (hypothesis 1, prediction 3) and were not successful mating partners based on the DNA fingerprinting data.

One confounding variable in this study is the low-ranking natal males' relatedness to the adult females. The three lowest-ranking natal males had close

**TABLE IV. Spearman Rank Correlation Coefficient of Agonistic Interactions Won by Females by Male Rank\***

	1-m radius	<i>P</i>	2-m radius	<i>P</i>	4-m radius	<i>P</i>
Males	0.611	0.000	0.362	0.015	0.175	0.281

\*Females gave either aggressive (A) or no (0) signals. Males gave only submissive (S) signals.

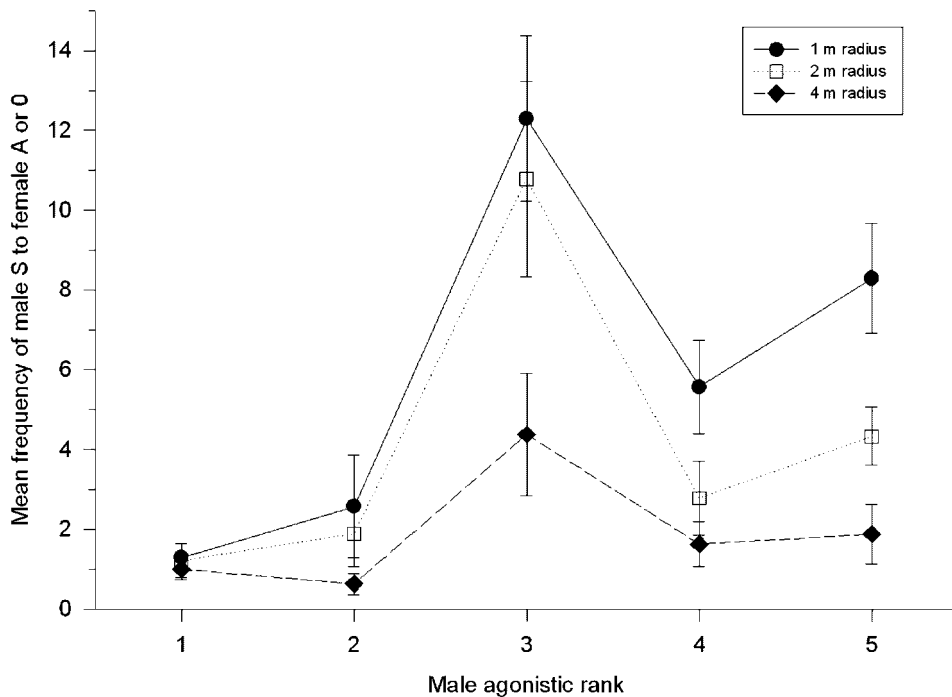


Fig. 3. Frequency of aggression received from each female by each male.

female relatives (sisters or niece) as well as more distant female(s) relatives (females from the other related matriline) in the group. Since it is rare for *L. catta* to mate with close relatives [Pereira & Weiss, 1991], this could affect the ability of these males to mate successfully. Their young age could also affect their ability to mate successfully. However, the second-ranking, unrelated, older male was also unsuccessful in siring offspring. This male was less deferent than the alpha male, by the definition used here, as he fed more than the alpha male at all radii lengths.

If the difference between the behavioral strategies of the high- and low-ranking males were not dependent on their age and relatedness to the females, these results would suggest that males change their behavioral strategies throughout their reproductive career. Low-ranking males may not be preferred as mates, and their access to resources would be limited by higher-ranking females and other males. As these males attain a higher dominance status, they can afford ecologically to defer to females because they displace younger, lower-ranking males from food sources. The low-ranking males in this study were also

the three youngest males in the study group. Maturing males in their natal group may also have limited mating opportunities due to female philopatry. As they mature and/or migrate to a new group [Sauther & Sussman, 1993], they may then achieve higher rank by challenging resident males to attain high rank and ultimately breed. Similar patterns have been observed in other captive populations [Pereira & Weiss, 1991]. However, Sauther [1993] found no equivalent result in wild populations, in which male–female aggression actually increased during times when females were most reproductively stressed. One possible explanation offered by Sauther [1993] for the differences between captive and wild populations is that because captive populations are provisioned with high-quality food, male deference is feasible.

In this study the degree of female dominance and female feeding priority increased with an individual's ability to monopolize food distributed in smaller circles (1 m and 2 m). Because equal amounts of food were presented during each trial, it appears that how food is dispersed (patch size) more directly influences the expression of female dominance than the amount of food present. Because food was contained in a smaller space, low-ranking males challenged females more frequently and females responded aggressively toward them. When food was distributed in circles with a 4-m radius, both males and females aggressed less and ate more.

This pattern may support explanations as to why *Eulemur fulvus rufus* does not express female dominance [Pereira et al., 1990]. Sussman [1974] found that *E. f. rufus* are more folivorous than *L. catta*. Therefore, since leaves are a more ubiquitous source of food than fruit, *E. f. rufus* females may not be as ecologically stressed as *L. catta* females. Furthermore, leaves are not as easily monopolized as fruit. In contrast, although *E. f. rufus* in southeastern Madagascar [Overdorff, 1993] are more frugivorous throughout the year, females are not dominant to males, as might be expected based on the results from this study. One possible explanation is that when fruit is most scarce, these study groups maintain a more folivorous diet (as did Sussman's study groups year-round). When fruit is available, it may be so abundant that the patches are large enough to be used by all individuals.

In conclusion, the male and female *L. catta* in this captive population showed different behavioral strategies depending on age, rank, and dispersal of food to meet daily energetic demands and reproduce. The highest-ranking, older male was deferent to females when they fed in small food patches, and was successful in mating. Presumably because of this deference, rates of aggression were low between females and high-ranking males. At the same time, female agonistic superiority (female dominance) was important in maintaining female feeding priority over nondeferencing, low-ranking related males when resources were limited in dispersion.

## ACKNOWLEDGMENTS

We thank the St. Catherine's Island Foundation and the New York Zoological Society (especially Frank Larkin, Royce Hayes, John Iderosa, and Bob Lessnau) for making this study possible. We thank Carel van Schaik, Ken Glander, Jayne Gerson, Kimberley Wood, Charles Nunn, Leslie Digby, and Nicholas Malone for stimulating discussions and comments on the manuscript. We thank the Molecular Genetics Department and the Forensics Department (especially Eddie Carden) of LabCorp for assistance and training in DNA fingerprinting. This is a Duke University Primate Center publication.

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