

## RESOURCE COMPETITION IN WILD POPULATIONS OF RINGTAILED LEMURS (*LEMUR CATT* A ): IMPLICATIONS FOR FEMALE DOMINANCE

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### ABSTRACT

Stresses imposed on female lemurs by adapting their reproductive events to seasonal resource availability may be exacerbated by high pre- and post-natal maternal investment and by group living. Within such a context female dominance can be seen as a critical behavior, enabling females to coexist with more than one non-natal male within a highly seasonal environment. Females may tolerate year-round male membership as males provide low-cost sentinels for predator detection and defense. Furthermore, male membership may be a viable reproductive tactic for both females and males, especially because females mate first with group males. A combination of female choice of small males and ecological and reproductive constraints on male size may have led to the current system of female dominance in ringtailed lemurs.

### INTRODUCTION

Although females form coalitions against males in many primate species (Smuts, 1987), true female dominance wherein an adult female consistently evokes submissive behavior from an adult male is rare. Among anthropoid primates there is some evidence that female *Cercopithecus talapoin* supplant males without female coalitions (Wolfheim, 1977), and among *Cebus olivaceus* the highest ranking female is dominant to all individuals, male and female, with the exception of the top-ranking male (Robinson, 1981).

Among lemuroid primates, true female dominance involving both feeding and nonfeeding contexts (Kappeler, 1990a) has been observed in captive and wild populations of *Lemur catta* (Taylor, 1986; Kappeler, 1990a; Sauther, 1992), but the existence of female dominance in other lemur species is less clear. It has also been reported for *Indri indri* (Pollock, 1979), *Propithecus verreauxi* (Richard and Heimbuch, 1975), *Phaner furcifer* (Charles-Dominique and Petter, 1980), *Microcebus murinus* (Perret, 1982; Pagès-Feuillade, 1988), *Varecia variegata* (Kaufman, 1991), and *Daubentonia madagascariensis* (Rendall, 1993). However, of these lemur species, only *I. indri*, *V. variegata* and *D. madagascariensis* exhibit some consistent directionality of agonism (see Pereira et al., 1990). None of these studies provide data for female dominance in nonfeeding contexts (e.g., over grooming partners, resting sites etc.),

making it difficult to differentiate female feeding priority from true female dominance (see Kappeler, 1990a). Furthermore, it is becoming clear that the expression of female dominance is variable among lemurs. For example, Sussman (1972) found no indication of a dominance hierarchy, and low levels of aggression in red-fronted lemurs, *Eulemur fulvus rufus*, a species similar in body size and proportions to *L. catta* (Tattersall, 1982), and Pereira et al. (1990) found no evidence of female dominance in any context for semi-captive or wild red-fronted lemurs.

Given the current uncertainty of the nature of female dominance among lemur species, it is important to determine the actual patterns of resource competition in the one lemur species which exhibits undeniable female dominance. This paper presents such information on free-ranging ringtailed lemurs.

## METHODS

### Study Site

Research was conducted at the Beza Mahafaly Special Reserve, which is located approximately 35km northeast of the town of Betioky. The area is dominated by *Tamarindus indica* in the eastern portion of the reserve, with dry-adapted species such as *Salvadora augustifolia* and *Euphorbia tirucalli* becoming more common as one moves to the west. The habitat is very seasonal, with a hot/wet season (December-April) associated with greater food availability as measured by the phenology of ringtailed lemur food resources, a cool/dry season (May-September) when food availability is dramatically reduced, and a transitional period (October-November), which is associated with increased availability of certain resources such as flowers. Rainfall is also seasonal with 506mm falling during the wet season. More details about the study site have been presented elsewhere (Sauther, 1989; Sussman, 1991).

The focus of the study was to document the feeding ecology of two groups of ringtailed lemurs living in a riverine forest within the reserve. A total of 16 *L. catta* (Black troop: 4 females, 2 males; Green troop: 5 males and 5 females) were studied, and 1800h of observations were collected and entered directly into hand-held portable computers.

### Behavior Patterns Sampled

The focal animal sampling method was used (Altmann, 1974). Behavioral categories were: feeding, resting, grooming, sunning, travel (movement as a group), moving (specified as to type, e.g., walk, run, etc.), defecating, urinating, and a category called standing, when the animal was between activities and was simply standing. All these behavior patterns were sampled at five minute intervals and the animal's location was noted. If the animal was feeding or foraging, the plant species and part used was also recorded. At 15min intervals the behavior and location of both the focal animal and its nearest neighbor were noted, and the distance of the nearest neighbor was recorded. Below, I will only consider nearest neighbor data from cases where both individuals were feeding. There were no consistent gender differences in nearest neighbor identity (see Sauther, 1992).

Agonistic behavior was recorded *ad libitum*, even if it did not involve the focal animal. Aggressive behavior included approaches, cuffing, biting, lunging, and chasing; submissive behavior involved retreating and running away with or without spat vocalizations. The behavioral context of all agonistic interactions was also recorded. Feeding agonism involved displacements from a food resource. Nonfeeding agonism included displacements over water, resting sites, or grooming partners. It included stinkfights (see Jolly, 1966) between males, but did not include this behavior when directed by males towards females, as this may be sexual in nature (Sauther, 1991a,b). Nonfeeding agonism also included social spacing, which were agonistic

events designed to increase the distance between two individuals, and which were not related to other contexts. Aggressive feeding agonism involved chasing, biting and cuffing, whereas non-aggressive feeding agonism included only approaches and retreats.

The behavior of each adult member was sampled one day per month for at least 7h. Continuous daily observations of both troops were made during the mating season, (May) and during the birth season (from late September through early November). Expected frequencies of agonistic interactions were calculated by multiplying the total number of agonistic episodes for each member for a given period (e.g., wet or dry season) by the expected proportions based on the number of male or female partners potentially available. Once expected frequencies were determined, a  $X^2$ -value was calculated for each pair of dyads (female-female (FF) versus female-male (FM); FM versus male-male (MM); FF versus MM). The significance of the  $X^2$ -value was determined by randomization and Monte Carlo procedures, which make no assumption about their distribution, using SAS and Quickbasic (Edington, 1980; Noreen, 1989; Manly, 1991).

## RESULTS

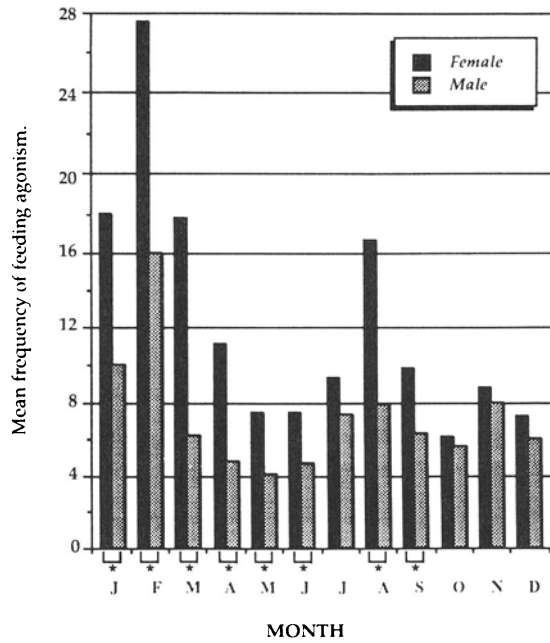
### Resource Competition

**Feeding Agonism.** Of the total agonistic events observed (2301), 86% occurred over access to food resources. The level of feeding agonism differed by gender. Females exhibited significantly greater mean frequencies of feeding agonism for most months than did males (Fig. 1). Feeding agonism between males and females peaked during the late lactation/weaning period (Fig. 2).

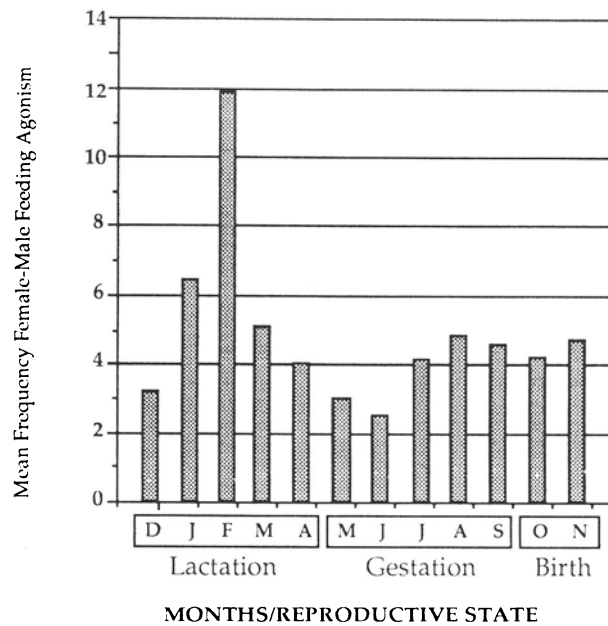
To determine how this agonism was distributed by gender, feeding agonism was separated into three dyads of FF, FM and MM for both Green and Black troop (Table 1). During the wet season, in both groups females exhibited more feeding agonism with each other than expected by chance. Males, on the other hand, suffered less feeding agonism from other males than expected in the larger Green troop, whereas the frequencies were as expected in the smaller Black troop. The two troops also differed with respect to FM agonism. In the larger group, FM agonism differed little from expectation, but in the smaller group, FM agonism was considerably less than expected. In the dry season FF agonism did not differ from expectation in the larger troop but was more than expected in the smaller troop. MM agonism was less than expected in the larger group, but more than expected in the smaller group. FM agonism was as expected in the larger troop but less than expected in the smaller troop.

Feeding agonism was split into aggressive (interactions involving chasing, biting and cuffing) and nonaggressive (interactions involving only approaches and retreats) (Fig. 3). Females showed greater mean frequencies of aggressive agonism than did males throughout the wet season, a period of relative food abundance, whereas they showed greater nonfeeding agonism during the dry period of reduced food availability. FM agonistic dyads plotted by month relative to the type of agonism indicate that for most months females aggressively displaced males from feeding patches (Fig. 4).

Agonism was compared by dyads relative to aggressive and nonaggressive feeding agonism. For all seasons, and in both troops aggressive FF feeding agonism was greater than expected by chance based on the number of potential female partners (Table 2). MM was reduced for both seasons in Green troop, but MM agonism was less than expected in the smaller Black troop during the wet season and greater than expected in the dry season. For the dry season in Black troop, and both seasons in Green troop, FM agonism differed little from expected. However, FM was less than expected in the smaller Black troop during the wet season.



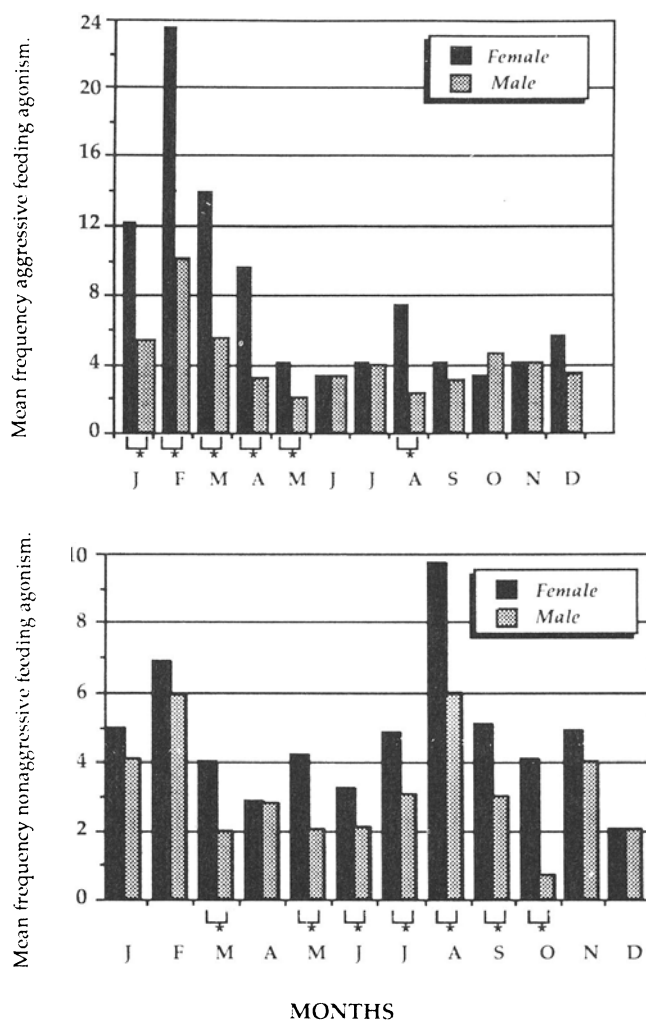
**Figure 1.** Sex differences in feeding agonism among ringtailed lemurs. \* indicates  $P < 0.05$ . Total feeding agonism:  $N = 1985$  bouts.



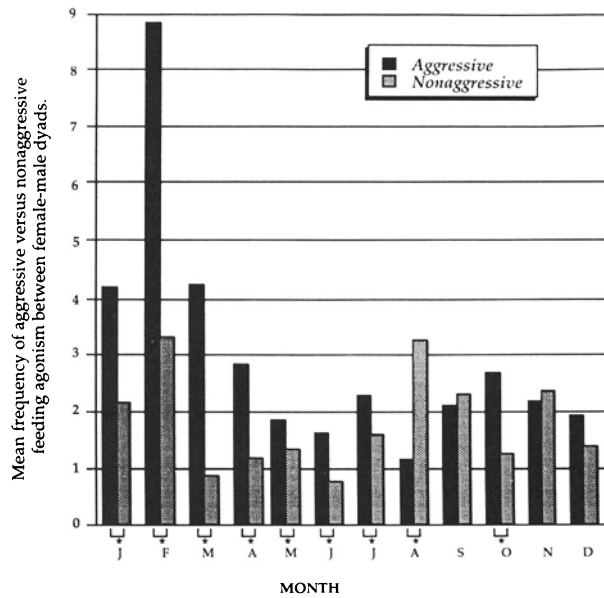
**Figure 2.** Female-male feeding agonism in ringtailed lemurs. Total female-male feeding agonism,  $N = 942$  bouts.

**Table 1.** Dyadic feeding agonism during the wet and dry season by troop. The number of observed agonistic interactions is presented for each dyad-class. FF = female-female dyads, FM = female-male dyads, MM = male-male dyads. \*P<0.05, \*\*P<0.01.

	<u>WET SEASON</u>			<u>DRY SEASON</u>	
<u>Dyads</u>	<u># Observed</u>	<u>X<sup>2</sup></u>	<u>Dyads</u>	<u># Observed</u>	<u>X<sup>2</sup></u>
<u>Green Troop</u>					
FF/FM	320/405	24.94**	FF/FM	160/225	0.28
FF/MM	320/67	35.28**	FF/MM	160/41	10.73*
FM/MM	405/67	11.04*	FM/MM	225/41	10.79*
<u>Black Troop</u>					
FF/FM	162/97	21.07**	FF/FM	138/84	17.81**
FF/MM	162/19	9.65*	FF/MM	138/24	25.73**
FM/MM	97/19	14.98*	FM/MM	84/24	22.70**



**Figure 3.** Sex differences in aggressive and nonaggressive feeding agonism among ringtailed lemurs. \* indicates P<0.05. Total aggressive feeding agonism; N=1208 bouts. Total nonaggressive feeding agonism, N=777 bouts.



**Figure 4.** Aggressive vs nonaggressive feeding agonism in female-male dyads. \*indicates  $P < 0.05$ . Total aggressive feeding agonism:  $N = 577$  bouts. Total nonaggressive feeding agonism,  $N = 335$  bouts.

**Table 2.** Dyadic aggressive feeding agonism during the wet and dry season by troop. See Table 1 for details.

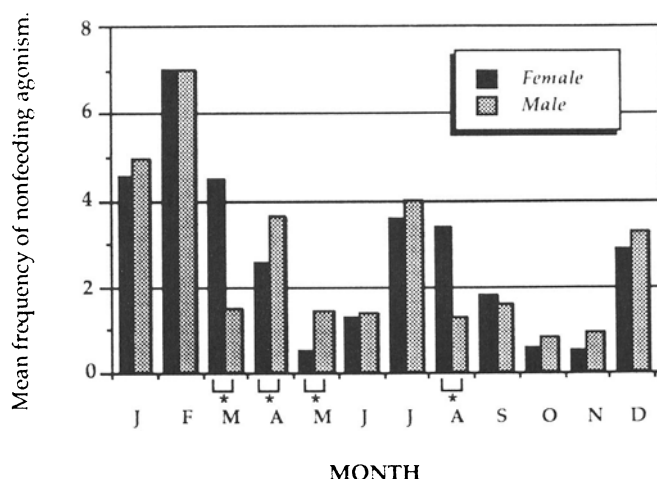
WET SEASON			DRY SEASON		
Dyads	# Observed	$X^2$	Dyads	# Observed	$X^2$
<b>Green Troop</b>					
FF/FM	264/304	30.55**	FF/FM	75/122	2.72*
FF/MM	264/38	34.15**	FF/MM	75/22	8.80**
FM/MM	304/38	34.15**	FM/MM	122/22	6.08**
<b>Black Troop</b>					
FF/FM	109/57	13.09*	FF/FM	55/34	6.67**
FF/MM	109/2	10.10*	FF/MM	55/6	9.56**
FM/MM	57/2	8.31**	FM/MM	34/6	3.11**

Nonaggressive feeding agonism among females was near expected frequencies for the wet season, but greater than expected during the dry season (Table 3). MM was as expected in the wet season, but varied between the two groups for the dry season. MM was less than expected in Green troop and greater than expected in Black troop. FM was as expected in Green troop but was less than expected in the smaller Black troop.

**Nonfeeding Agonism.** Only 14% of the total agonism observed could be categorized as nonfeeding agonism. Sexually mature, reproductive females decidedly won all such encounters with males (but see below). Comparing males and females, nonfeeding agonism was more variable than feeding agonism, with males actually surpassing females during April and the mating period in May (Fig. 5). When broken down by context, most nonfeeding agonism (52%) was over access to water, which collected in tree hollows. Some nonfeeding agonism also occurred in the context of social spacing (23%), over access to favored resting sites (10%), and stinkfights between males (7%).

**Table 3.** Dyadic nonaggressive feeding agonism during the wet and dry season by troop. See Table 1 for details.

WET SEASON			DRY SEASON		
Dyads	# Observed	X <sup>2</sup>	Dyads	# Observed	X <sup>2</sup>
<u>Green Troop</u>					
FF/FM	56/101	0.49	FF/FM	85/103	10.69**
FF/MM	56/29	1.20	FF/MM	85/19	15.37**
FM/MM	101/29	0.49	FM/MM	103/19	7.18**
<u>Black Troop</u>					
FF/FM	53/40	5.57*	FF/FM	83/50	15.03**
FF/MM	53/17	1.45	FF/MM	83/18	17.48**
FM/MM	40/17	5.02	FM/MM	50/18	22.55**



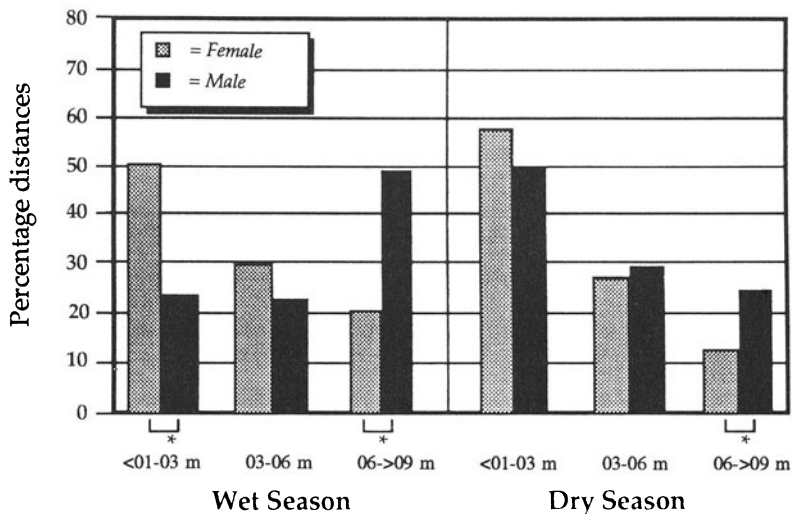
**Figure 5.** Sex differences in nonfeeding agonism among ringtailed lemurs. \* indicates  $P < 0.05$ . Total nonfeeding agonism,  $N = 313$  bouts.

**Displacements Of Females By Males.** During the course of the study a total of 35 displacements, or 3% of the total agonism between females and males, involved males displacing young adult, nulliparous females who were two years old at the start of the study (November, 1987) (Table 4). All but one of these were nonaggressive in nature; either a male approached a female and she retreated, a male took a food item (e.g., a *Tamarindus indica* fruit) from her, or a male displaced a female from a drinking site by moving her aside with his body. Most of these displacements were over food or water resources. Only one interaction could be characterized as aggressive. During the mating season, males would continuously approach females to monitor their receptivity, and if they were not cuffed or otherwise discouraged by the female, they would try to mate with her (Sauther, 1991b). On one occasion the top-ranked male of Green troop approached one of the young females, and when she did not cuff him away, he attempted to mount her. A brief jumpfight ensued, the female cuffed the male, he cuffed her, and he jumped away. There were no cases where a young female approached a male and he refused to leave the feeding site. All of these displacements occurred between November, 1987 and the mating season in May, 1988. Males were no longer able to displace these females after their first mating season.

**Table 4.** Context of male wins over females for ringtailed lemurs.

Context of Male's Win	Frequency	Percentage of Total Male Wins	Percentage of Total Agonism between Females and Males
Feeding	16	45%	2%
Drink/Lick	10	29%	1%
Social Spacing	5	14%	0.005%
Resting Sites	3	9%	0.003%
Sexual	1	3%	0.001%
<b>TOTAL</b>	<b>35</b>		<b>3.09%</b>

**Nearest Neighbor Distances During Feeding.** One potential source of feeding competition is having close neighbors during feeding bouts. Spatial relationships during feeding can presumably affect feeding efficiency, and close neighbors could limit resource availability. Males differed from females with regard to how close they fed to others (Fig. 6). Males tended to spread out and feed farther away from other individuals. During the wet season, males had greater percentages of "distant" nearest neighbors (>6m), whereas females had higher percentages of "close" nearest neighbors (<3m).

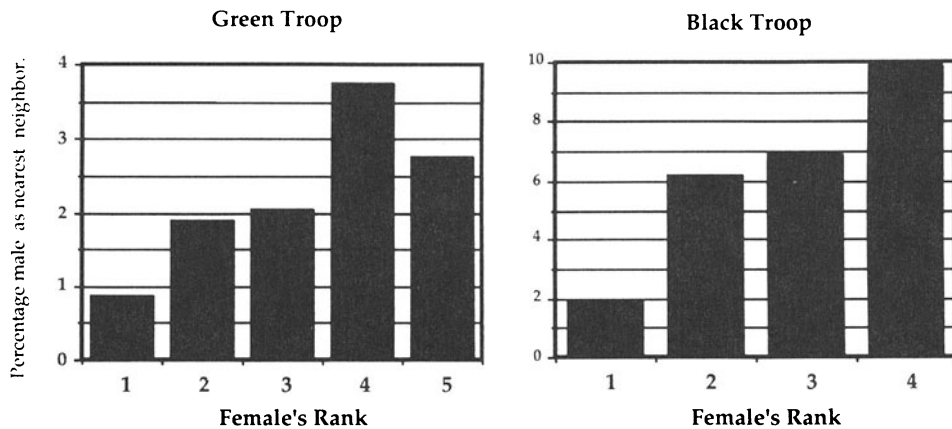
**Figure 6.** Proximity of nearest neighbors while both feed. \* denotes  $P < 0.05$ .

During the dry season males and females had similar percentages of close nearest neighbors during feeding although males still had greater percentages of distant nearest neighbors. Comparing the wet and dry season, males more than doubled their time spent feeding near others. This tendency to feed closer in the dry season was most likely the result of the availability of resources, which tended to be limited to small patches of herbs or single fruit trees.

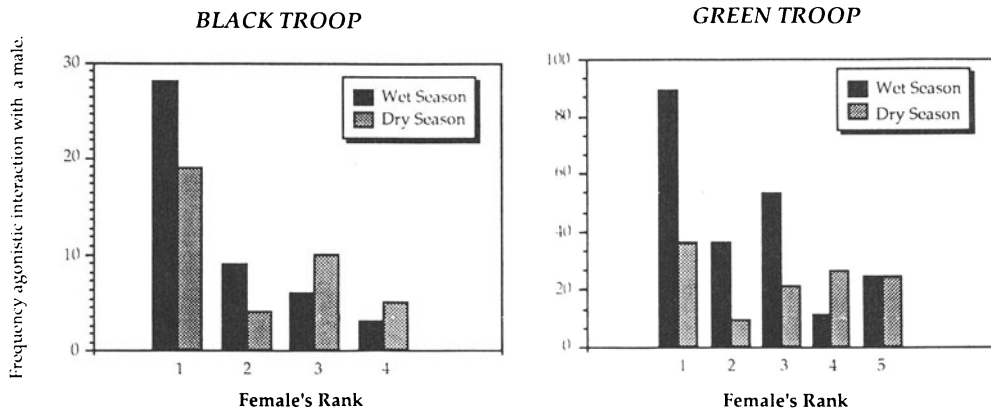


To establish whether all females were equally impacted by the closer proximity of foraging males during the dry season, the percentage of time males spent near individual females was determined (Fig. 7). In both groups males tended to feed most often near low-ranking females. Relative to the wet season, this resulted in low-ranking females maintaining or increasing agonistic bouts with males during the dry season, whereas high ranking females decreased such agonism (Fig. 8).

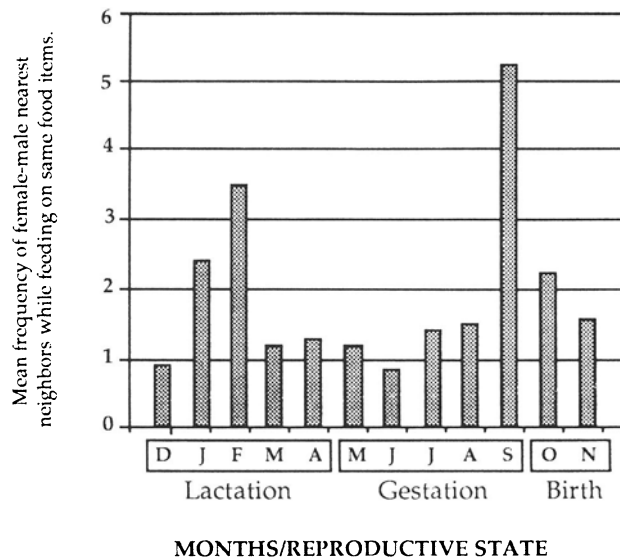
Another measure of direct feeding competition by males was the frequency that the nearest neighbor fed on the same food item and part. Figure 9 shows the mean frequency per month that females had males as nearest neighbor who were also feeding on the same species and plant part. Two peaks occurred, one during late lactation/early weaning, and the other during late pregnancy-birth-early lactation.



**Figure 7.** Percentage of time females and males were nearest neighbors during foraging and feeding in the dry season.



**Figure 8.** Comparison of female-male feeding agonism by season and female's rank.



**Figure 9.** Feeding bouts where a female had a male as a nearest neighbor, and both were feeding on the same food item, N=381 bouts.

## DISCUSSION

### Function and Evolution of Female Social Dominance In Ringtailed Lemurs

As already noted, female dominance among lemur species is not as ubiquitous as once thought (e.g., Pereira et al., 1990). For most lemur species, we currently lack the appropriate ecological and behavioral data which would clarify the nature of female dominance in free-ranging groups, e.g., how synchronous is female reproduction, what is the degree of resource seasonality, and what is the frequency and context of male displacements by females. Nevertheless, there are currently three arguments to explain social dominance among lemurs: paternal investment (Pollock, 1979), male deference as a reproductive strategy (Hrdy, 1981; Pereira et al., 1990), and high reproductive costs (Jolly, 1984; Young et al., 1990). As already noted by Young et al. (1990), paternal investment is a possibility only for monogamous species. Is there any support for the latter two hypotheses with regards to free-ranging *L. catta* behavior and ecology?

### Male Deference

With regard to male foraging strategies, Hrdy (1981) has suggested that in female-dominant species males may defer to females in feeding contexts to save energy for mate competition. Males should therefore concentrate on conserving energy and engage in intense male-male competition only during the brief breeding season. This makes sense only if rank-related advantages are limited to the mating season, and seems to assume that feeding agonism among males is not important.

*L. catta* has been presented as a species to fit Hrdy's model (Jolly, 1984). Under such a scenario, male ringtailed lemurs would maintain themselves at minimal levels of feeding competition in the dry season, when food is limited, and then compete for food and status when food availability increases just prior to the mating season. This model is not tenable for a number of reasons.

First, rank-related advantages were not limited solely to the breeding season. High-ranking, central males used less expensive forms of locomotion, they had greater access to drinking sites than lower-ranking males, they won more agonistic bouts over food, and they fed more, by weight, on "valuable" but limited foods such as some fruits (Sauther, 1992). Second, male-male agonism does not support the contention that males were "saving themselves" during the lean period. Males maintained similar mean frequencies of feeding agonism with each other during each season (lactation season = 15; gestation season = 13; birth season = 15;  $P > 0.05$  for all pairwise comparisons). Third, there is no indication of male "chivalry" (sensu Jolly, 1984) with regards to lessening female feeding pressure. The frequency of female-male feeding agonism remained similar throughout most of gestation and the birth season. Furthermore, it dramatically increased at a time when females were most stressed, i.e., during the late lactation/weaning period.

Pereira et al. (1990), found some support for Hrdy's argument among captive ringtailed lemurs. They found that most agonistic "wins" (75%) by females over males involved no aggression, simply approach-retreat interactions, and they suggested that females might choose to mate with deferring males. However, in the present study on free-ranging populations, there was no indication that males were simply deferring to females in feeding contexts. Females had feeding priority over males because they actively usurped males from feeding sites. Females would not hesitate to chase males from a feeding site, and retribution for a slow responding male could be quick and violent. For example, on one occasion a female feeding in a tree grabbed the shoulders of a lingering male, held him in place, and bit him soundly on the top of his head. Over 63% of all feeding agonism between males and females involved a female aggressively displacing the male. In addition, during most months females continued to employ more aggressive, rather than nonaggressive forms of feeding agonism when displacing males from feeding sites. It is possible that the pattern of greater active, aggressive feeding agonism observed in the wild populations was absent in the captive population due to provisioning.

Males could defer to females indirectly, by simply feeding further away from them. However, in this study males fed more closely to females, and directly competed with them by focusing on the same foods during two critical reproductive stages, late lactation/early weaning and late pregnancy/early lactation. Furthermore, all individuals, regardless of gender, fed more closely to one another during the dry season, a period of low food availability. Thus, evidence from the current study provides no indication of male deference in ringtailed lemurs.

### **High Reproductive Costs**

Both Jolly (1984) and Young et al. (1990) have made the case that especially high reproductive costs among lemurs might explain the evolution of female dominance in these species. Specifically, a number of lemurs combine low basal metabolic rates with high prenatal maternal investment (Young et al., 1990), and they produce altricial neonates which must be supported by the mother during their infant's rapid postnatal growth period (Jolly, 1984). In addition, many lemur species exhibit seasonal reproduction (Jolly, 1984). Ringtailed lemurs exhibit one of the most highly constrained mating seasons, approximately 24h (Evans and Goy, 1968), with all females within any one troop breeding during a short period of 1-3 weeks (Jolly, 1966; Sussman, 1977; Sauther, 1991b). At Beza Mahafaly this strict breeding seasonality is tied to the availability of resources (Sauther, 1993). Females lactate during the period of food abundance (the wet season, December-April), gestate during the period of relatively low food availability (May-September), and give birth during peaks of important food resources such as flowers (October-November). Given the close reproductive synchrony in this species (Jolly, 1966; Pereira, 1991; Sauther, 1991b) reproducing females will experience identical reproductive events and undergo similar reproductive stresses leading to high levels of interindividual resource competition (Sauther, 1993). Under such conditions, extra feeding competition from group males would be a distinct disadvantage not only to females, but also to their infants, unless adult females had feeding priority. Female dominance might develop

under such conditions to mitigate male resource competition. Results from this study support this argument.

**Female Feeding Investment.** Gender differences in resource competition should reflect greater feeding investment by females, i.e., if food is a more limited resource for females (*sensu* Wrangham, 1980) females should expend more energy in its acquisition. This was seen for *L. catta* at Beza Mahafaly. Not only were females involved in more feeding agonism than males throughout most of the year, but they also engaged in more expensive (i.e., aggressive) forms of contest competition such as chasing, cuffing and biting during the critical lactation period.

**Female Feeding Stress.** Given their reproductive role, females should be under greater feeding stress than males. During lactation, which is the most costly reproductive state for placental mammals (Sadleir, 1969; Robbins, 1983; Clutton-Brock et al., 1989), female ringtailed lemurs were displacing each other at higher frequencies than would be expected, and more of these displacements were aggressive in nature. Males, on the other hand, either received expected or less than expected feeding agonism from other males. During gestation, high frequencies of aggressive and nonaggressive displacements continued between females. In addition, females had greater percentages of close neighbors during feeding throughout the year, whereas males tended to spread out and feed further from others during the wet season.

**Feeding Competition From Males.** Males were costly competitors for females. They did not simply retreat from feeding patches, and if the food item in question was portable (e.g., *Tamarindus indica* fruit), males could run off with the fruit in their mouth. In most cases females had to aggressively displace males from a feeding site, albeit males never contested such displacements. Due to their tendency to feed on identical food items near females, males provided females with both direct and indirect feeding competition especially during the two periods of expected maximal stress, late gestation/early birth, and late lactation/early weaning. Feeding near other individuals can be costly as it increases the chances of aggressive displacements (Mori, 1977; Furuichi, 1983) and can limit foraging success (Robinson, 1981). In addition, male feeding competition was especially acute for lower-ranking pregnant females who had to contend with close male feeding proximity during the period of lowest food availability. This resulted in low ranking females increasing feeding agonism directed at males, unlike high ranking females who actually decreased male-directed feeding agonism relative to the wet season.

There is also evidence that females living in groups with fewer males have an advantage in terms of feeding agonism. Black troop had only two resident males, whereas Green troop had five. Female-male feeding agonism, both aggressive and nonaggressive, was consistently less than expected for most seasons in the group with fewer males, whereas it was at expected levels in the group with more males.

**Nonfeeding Agonism.** It has been suggested that this model, which focuses on high reproductive costs, does not account for female dominance in nonfeeding contexts, which have been observed among captive populations of ringtailed lemurs (Kappeler, 1990a). In this study while female dominance in nonfeeding contexts was also observed, the majority of these were over important resources such as drinking sites, and thus fits with the reproductive energetics model. The second most frequent context was social spacing. If, as is argued here, males compete with females for resources, maintaining social distance from other individuals (including males) may help alleviate direct resource competition for females. It is not possible to currently reject the premise that female dominance in nonfeeding context may also relate to female reproductive costs.

### **Lemurs Not Exhibiting Female Dominance: The Case of *Eulemur fulvus rufus***

As already noted, not all lemurs exhibit female dominance. Pereira et al. (1990) found no evidence of female dominance in either captive or free-ranging groups of *E.*

*fulvus rufus*. However, overt expression of female dominance may be tied to the availability of resources. Although red-fronted lemurs are sympatric with ringtailed lemurs in limited areas, field studies on both free-ranging and semi-free-ranging populations indicate that *E. fulvus rufus* is adapted to continuous canopy forests, but that *L. catta* can exist alone in drier brush and scrub forests, and is thus adapted to a more variable environment (Sussman 1972; Ganzhorn, 1985). These two species overlap only in mixed forest which contain both types of forest (Sussman, 1972). Furthermore, distributions of ringtailed lemurs are restricted to the drier southwestern and southern portion of Madagascar, whereas red-fronted lemurs are found in the more moist western and eastern portions of the island (Tattersall, 1982). Both Sussman (1974) and Ganzhorn (1985) have suggested that red-fronted lemurs are adapted to more stable environments (i.e., foraging in continuous canopy where resources are more abundant and evenly distributed), whereas ringtailed lemurs are adapted to a more variable environment (i.e., drier, more seasonal forests where foods are sparsely distributed). Within this highly seasonal environment, *L. catta* females may also suffer greater post-natal maternal costs than *E. fulvus rufus* females, because ringtailed lemur infants exhibit a more precocial rate of development (Sussman, 1977). While red-fronted lemurs may encounter less feeding pressure, leading to low levels of agonism and more egalitarian social relationships, ringtailed lemur females incur high reproductive costs which are exacerbated by foraging on discrete patches of seasonal resources. This may lead to greater feeding agonism and a more overt expression of female dominance in this species.

### **Male Displacement of Females**

Female dominance in ringtailed lemurs is a developmental process in which females in a troop must eventually alter their relationship with adult males. Female infants may be buffered from male feeding competition by feeding near their mothers. During this period they can take food from males with impunity, although males will not hesitate to steal food from weaned infants if the mother is not in sight. Once weaned, males can and do displace females, but these displacements are not aggressive in nature. As the female reaches sexual maturity, her relationship with males goes through a transitional process which appears to be mitigated by male sexual advances. As noted elsewhere (Sauther, 1991b), during the mating season males continuously approach females to monitor their receptivity. Young females are thus "forced" to interact aggressively with males in order to thwart mating attempts prior to their receptive period. After the mating season, this new relationship expands to other, non-sexual contexts, i.e., feeding. Once this transitional period is over, males appear unable (or unwilling) to attempt such displacements, and females begin to displace males on a regular basis. One of the consequences of this process is that young females may incur higher levels of male feeding competition just prior to their first mating season.

### **Multimale Membership in a Female Dominant Species**

Why do males live together in multi-female groups wherein they suffer feeding agonism from all adult females, instead of forming all-male groups or foraging as solitary males? Not surprisingly, multi-male membership is most likely tied, in part, to tactics for increasing reproductive success. Both Andelman (1986) and Altmann (1990) have noted a positive relationship between the number of females in a group and the number of group males. This is also seen at Beza Mahafaly, where the number of males in a troop is significantly positively correlated with the number of adult females ( $r=0.78$ ,  $P<0.01$ ;  $N=70$ ). This is most likely a reproductive strategy, i.e., more adult females mean more potential mates. Among ringtailed lemurs, there is evidence that establishing close relationships with troop females may provide a reproductive advantage. It is likely that males use olfactory cues from females to determine the onset of estrus (Jolly, 1967; Schilling, 1979) since behavioral cues from females only occur when she is receptive (Evans and Goy, 1968; Sauther, pers. obs.). Males occupying a high-ranking, central position are able to maintain a closer relationship with females to monitor their reproductive state, they can limit

monitoring by other males, and they are the first to mate (Sauther, 1991b). Being a female's first mating partner may be critical, as there is evidence from captive studies of ringtailed lemurs that mating with ejaculation leads to a loss of receptivity (Evans and Goy, 1968; van Horn and Resko, 1977). Furthermore, although females will mate with nongroup males, group males are able to mate first (Sauther, 1991b). In addition, there may be a first mate advantage in this species (Pereira and Weiss, 1991). Therefore, living within a social group may increase a male's chances for successful matings, and males may attempt to transfer into troops where they can acquire the central position.

Male membership in a group may also help buffer males from nutritional stress, and predation. There is evidence that migrating males at Beza Mahafaly may be under higher levels of nutritional stress (Sussman, 1991). Three males of an all-male group (which included both old and young adults) weighed significantly less than other group-living males. In addition, during the study one adult male was found dead and observations of the remains showed signs of predation (Sauther, 1989). It is possible that this male was in the process of migrating, as the remains were found outside the normal home range of his group.

Because troop males are food competitors, especially for lower-ranking females, why do females tolerate more than one non-natal male? Three suggested advantages of a multi-male membership are intergroup resource defense (Wrangham, 1980), predation detection and defense (Leutenegger and Kelly 1977; Busse, 1976; but see Cheney and Wrangham, 1987) and female reproductive success. As already noted, reproductive events appear to be tied to the availability of critical resources between late pregnancy and weaning in ringtailed lemurs. Under such conditions, successful intergroup agonism over access to resources may provide females with a reproductive advantage, and males could improve intergroup competitive abilities. However, among the ringtailed lemur groups observed, males were less involved in intergroup encounters, and often fed on resources while females fought (Sauther, 1992).

*L. catta* are semi-terrestrial and are therefore exposed to a number of terrestrial as well as arboreal predators (Sauther, 1989). Antipredator defense in this species involves vigilance and mobbing behaviors (for aerial predators) once potential predators are sighted. Throughout the study when predators such as raptors were encountered males took an equal or greater role in approaching, and even climbing into trees where such predators were perched. Furthermore, male attention is not focused on infants, allowing them to be more aware of potential dangers in the environment, especially since they tend to feed away from the main core of females. In this sense, males may provide lower-cost sentinels, because increasing the number of females would increase female-female competition for resources due to reproductive synchrony (c.f. Terborgh and Janson, 1986).

A third possibility may be tied to female reproductive success. The common view is that reproductive females are limited resources for which males compete (Trivers 1972; Wrangham, 1980), and that females should primarily be concerned with access to resources which may more directly affect their reproductive success. However, in a species with a highly constrained breeding period such as *L. catta*, female reproductive success may converge with that of males. Among free-ranging *L. catta* all females within a group experience estrus within 1-3 weeks of each other. There is also strong evidence that ringtailed lemur females living within the same forest enter estrus during similar periods. At Berenty Reserve females in four troops of ringtailed lemurs were either observed mating or showed physical signs of estrus (i.e., flushed and swollen genitalia) between April 16 and May 1 (Jolly, 1966). At Beza Mahafaly Reserve mating by females in four separate groups were observed between May 7 and May 26 (Sauther, unpubl. data). With such a large number of females entering estrus during the same short period, males could potentially become swamped and some females might not conceive during their first estrus. Ringtailed lemur females who do not conceive during the first estrous period will not have a second estrous cycle till 40 days later (Evans and Goy, 1968; van Horn and Resko, 1977) and a third cycle may occur 80 days after the second estrous period (van Horn and Resko, 1977). Late births will occur if females are fertilized during this second cycle, which can result in early weaning or weaning during food scarcity which creates undue stress on the infant and the mother. In this study even infants conceived during the first estrous

period, but born two weeks later than others were at a distinct disadvantage compared to other infants due to rapid infant development. In both troops these were infants born to lower-ranking multiparous females. For example, during troop progressions such infants attempted to be carried at a time when other infants were moving independently. On numerous occasions these infants also lagged behind the rest of the group, and lost contact with their mothers, who had to come back and retrieve them. Such infants were also required to compete with other infants whose foraging skills were more advanced. Both of these infants disappeared by the beginning of the dry season.

Male group membership may therefore increase reproductive success for both females and males. From the male's perspective, living within a group both increases a male's chance to successfully mate, and to mate earlier than non-group males due to female choice. Furthermore, close male contact may facilitate the onset of estrus in female ringtailed lemurs (Evans and Goy, 1968). Because *L. catta* females have such a narrow reproductive "window", mating with many group males who are immediately available during their restricted estrous period may lead to successful fertilization, avoidance of secondary estrus, and increase their chances of producing viable offspring. Thus females may tolerate a number of non-natal males, but the higher levels of aggression shown by lower-ranking females toward group males indicates that there may be a disparity in the number of males that females of differing ranks may tolerate.

### **Sexual Selection and the Evolution of Female Dominance in *Lemur catta***

Among most sexually dimorphic species, larger male size confers feeding priority over females (Smuts, 1987). However, female dominance in ringtailed lemurs is accompanied by a lack of sexual size dimorphism (Kappeler, 1991; Sussman, unpubl. data). If, as is argued here, females face high reproductive costs, and males do not defer to females in feeding contexts, then females must be able to aggressively displace males from feeding sites. It is thus feasible that female choice of small males may have occurred. In addition to female choice, body size in male ringtailed lemurs may also be constrained by reproductive energetics associated with seasonal reproduction. Kappeler (1990b) has made the important point that for smaller species such as lemurs, large body size in males might not be feasible in seasonal environments. Males do appear to be under constant feeding stress throughout the year, either from females or from other males. Furthermore, Clutton-Brock (1985) has suggested that if size dimorphism is not important in intra-male competition, other characteristics will be selected for. Kappeler (1990a) has proposed that agility may be more important than large body size for reproductive competition among male lemurs. Another essential characteristic is endurance. Sauther (1991b) observed the mating season among free-ranging *L. catta* at Beza Mahafaly, and noted that male-male competition for females involved great physical exertion, including climbing up and down trees, and protracted chases involving spectacular leaps. Furthermore, males were repeatedly interrupted during coitus, requiring the male to dismount and chase away other males as many as 25 times prior to ejaculation. In addition, this vigorous behavior occurred during a period of high temperatures (average = 37°C.). After the mating season males had visibly lost weight and appeared nutritionally stressed. Smaller, but physically agile and enduring males may therefore have a reproductive advantage in direct mate competition with other males, as well as being more attractive to females.

### **Conclusions**

These results support the contention that female dominance in ringtailed lemurs is a response to high reproductive costs which are exacerbated by a stressful, seasonal environment (Jolly, 1984; Young et al., 1990). The patchy distribution, and seasonal nature of food resources, have led to highly synchronized reproduction in this species. While this allows all females to lactate and wean their infants during a period of relative food abundance, it also results in greater feeding competition among females. Females not only compete with other troop females for access to resources, they are

also the main participants in intergroup encounters over important seasonal resources (Sauther, 1992). Although males are able to alleviate some feeding pressure to themselves by feeding further away from others, and by seeking out more displaced foods (Sauther, 1993), for females, reproductive costs make such a strategy less viable. Instead, ringtailed lemur females respond to greater feeding pressures, as well as to reproduction during periods of fluctuating resource availability, by exhibiting greater feeding investment which takes the form of direct resource (contest) competition. In this species, male feeding competition is mediated by female dominance. Females actively and aggressively maintain priority of access to resources. Males provide females with direct and indirect feeding competition which coincides with periods of costly reproductive states such as lactation, and periods of low food availability, such as the dry season. All females are affected, but lower-ranking females face dual competition from both males and higher-ranking females. For such females, and their just weaned infants, female dominance may be especially critical.

## ACKNOWLEDGEMENTS

A number of people deserve recognition for their help during the course of this study. I wish to thank Jeff Kaufmann, Behaligno, and the reserve guards for their assistance at Beza Mahafaly. In addition I wish to thank Mme Berthe Rakotosamimanana, Benjamin Andriamihaja, Joseph Andriamampianina, Pothin Rakotomanga, Mark Pidgeon and Sheila O'Connor, all of whom shared their expertise and help. My gratitude also goes to the Ministry of Higher Education and the School of Agronomy of the University of Madagascar. I would also like to thank R.W. Sussman, B.A. Hayes, P. Kappeler, J. Ganzhorn, D. Overdorff, C. Hildebolt, and an anonymous reviewer for helpful comments on an earlier draft, and J. Cheverud for his help on the randomization procedure. This project was funded by NSF Grant #BNS-8619240, a Fulbright Collaborative Grant, a grant from the National Geographic Society #3619-87, the Leakey Fund, and a fellowship from the American Association of University Women.

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