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**The effect of reproductive state, social rank and group size on
resource use among free-ranging ringtailed lemurs (*Lemur catta*)
of Madagascar**

Sauther, Michelle Linda, Ph.D.

Washington University, 1992

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The Effect of Reproductive State,
Social Rank and Group Size on Resource Use Among Free-ranging
Ringtailed Lemurs (*Lemur catta*) of Madagascar

by

Michelle Linda Sauther

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the requirements for the degree
of Doctor of Philosophy

May 1992

Saint Louis, Missouri

GEN

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1992

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ABSTRACT

Female primates incur higher reproductive costs than do males, therefore group living may be expected to create greater levels of resource competition among females. The Lemuriformes show a high degree of maternal investment which may be exacerbated in the ringtailed lemur, *Lemur catta*, which inhabits the drier, more seasonal riverine forests of southern Madagascar. How ringtailed lemur females respond to such stresses depends on a number of ecological factors. At the forefront is the distribution and availability of resources, which in this study determined the expression of rank advantages, the value of intergroup resource defense, and reproductive seasonality. Reproductive events appear tied to the availability of important resources. Thus females lactated and weaned their infants during a period of relative food abundance, but gestated during reduced food availability. Within each reproductive state females utilized numerous behaviors to reduce reproductive stresses. Lactating females employed a more energetically conservative feeding strategy by resting more, and by focusing on high-protein foods that were less costly to forage for. They also avoided feeding near one another, and spent more time feeding solitarily. Pregnant females decreased activity by resting and by decreasing social activity. Rank-related feeding advantages were mediated by resource distribution. Only resources which were monopolizable showed clear rank effects. However, high rank may confer feeding advantages to adult offspring, who feed closer to their mothers and may therefore be buffered from feeding agonism. Intergroup encounters are intimately related to an increase or decrease in the availability of resources, with flowers and fruits being the most contested items. This species' habitat contained resources which showed predictable, seasonal variability in abundance, which may promote birth seasonality in this species. If reproductive costs are high enough, unusual forms of female-male relationships may occur. Within this context female dominance in ringtailed lemurs may preserve a polygamous social structure and all the advantages it confers, while limiting feeding competition received from males. Such effects should not be viewed as unique to only certain groups (i.e. the Lemuriformes), but rather as adaptations to a particular suite of ecological constraints.

FOR ARMINE AND ANNIE

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CHAPTER 1

INTRODUCTION

Many diurnal primates live in groups, yet within a particular population group members can vary by age, gender, reproductive state, health, and social status. How these factors affect the behavioral dynamics of individuals is a difficult issue as many of the qualities can also work in combinations which have yet to be documented or understood. Nevertheless, selection occurs at the individual level, and therefore the ways in which ecological and personal characteristics affect individual reproductive success is key to understanding larger issues such as the cost and benefits of group-living, and proximate and ultimate causes of social organization.

Clutton-Brock (1977a) edited a seminal volume which, among other topics, sought to address how intraspecific variability might affect primate feeding ecology. Based on this and other field and laboratory studies, at least five important factors leading to interindividual differences in resource use among primates have been identified: sexual dimorphism, gender, reproductive state, social status, and age.

Sexual dimorphism creates interindividual differences in food sources utilized (Waser, 1977; Demment, 1983), or in foraging sites used (Rodman, 1977; Robinson, 1981). Reproductive state also affects feeding behavior. Captive studies indicate that female nonhuman primates change their feeding behavior during the menstrual cycle (Krohn and Zuckerman, 1938; Gilbert and Gillman, 1956; Czaja, 1975, Rosenblatt et al., 1980; Bielert and Busse, 1983), during pregnancy (Czaja, 1975; Kemnitz et al., 1984; Kirkwood and Underwood, 1984; Sauther, 1984) and during lactation (Kirkwood and Underwood, 1984; Sauther, 1984; Roberts et al., 1985). Increasing energy intake associated with lactation has also been observed (Sauther and Nash, 1986; Kirkwood and Underwood, 1984; Roberts, et. al., 1985; Blackburn and Calloway, 1976). Food intake may change during pregnancy (Silk, 1987a; Stacey, 1986), and lactating females may concentrate on more protein-rich

food sources, such as young leaves and invertebrates (Gautier-Hion, 1980; Harrison, 1983b).

Gender differences in feeding behavior may or may not be related to reproductive state. Females may spend more time feeding on insects and young leaves (Pollock, 1977; Waser, 1977), and invertebrates (McGrew, 1979; Robinson, 1981; Uehara, 1984) and may differ from males in the use of the same food sources (Teleki, 1975; Nishida et al., 1979; Boesch and Boesch, 1981; Muskin and Fischgrund, 1981; Takahata et al., 1984).

Age differences in feeding behavior also occur, with younger individuals spending more time feeding than adult members (Pollock, 1977), emphasizing certain food items (Waser, 1977) and using certain feeding sites more often (Fossey and Harcourt, 1977; Clutton-Brock, 1973)

Finally, social status may affect feeding behavior. Among certain lemur species females have priority of access to feeding sites (Richard, 1977; Pollock, 1979; Taylor, 1986). Higher-ranking individuals can have greater access to clumped food resources (Whitten, 1983) or water resources, (Wrangham and Waterman, 1981) or to food items in general (Watts, 1985).

Interindividual differences in resource use may thus be affected by a number of factors, but how each factor affects feeding variability is less clear. For example, Harrison (1983b) found sex differences in vervet feeding behavior (*Cercopithecus aethiops sabaeus*). According to Harrison during the dry season males, due to their "superior competitive ability", (larger body size) are able to maintain priority of access to flowers and fruit and subsequently fed on these food sources more than females. As a result, females concentrate on what he termed "secondary choice" foods such as leaves, grasses and herbs. However such foods may not be secondary choice because females were pregnant and lactating at this time, and concentrating on these protein-rich foods may have been related to reproductive state, a tendency also found by Gautier-Hion (1980). In this case the effects of social status and reproductive state are not separated, making it difficult to come to any conclusions about how either affects feeding behavior.

INTRASPECIFIC STUDY OF *LEMUR CATT*A

To evaluate the effects of social status, reproductive state and gender on resource use, a study of interindividual variability was carried out on two troops of free-ranging ringtailed lemurs in southern Madagascar. Only three studies have addressed the feeding behavior of free-ranging *Lemur catta* (Jolly, 1966; Sussman, 1977; Budnitz, 1976), but none of these focused on interindividual differences.

Populations of *L. catta* are found only in the drier forests of southern Madagascar (Tattersall, 1982). Group size averages between 9-22 (Jolly, 1966; Sussman, 1974; Budnitz and Dainis, 1975, Sussman, 1991). Linear dominance hierarchies exist for both sexes (Budnitz and Dainis, 1975; Taylor, 1986). Females form the stable core of the troop, and male transfer occurs (Sussman, 1991). Home ranges of *L. catta* troops vary; at Berenty they ranged from 6-23 ha (Budnitz and Dainis, 1975) while at Beza Mahafaly Special Reserve the size is much greater (26-32 ha) (Sussman, 1991). This species is semi-terrestrial. The two study troops spent over 1/4 of their time on the ground (Black Troop 26%, Green Troop 27%), which is similar to the results reported by Sussman (1972) at two other sites in southern Madagascar (Berenty 36%, Ansterananomby, 30%). Feeding on the ground also occurs frequently.

L. catta exhibits a number of characteristics that make them a good species for a study of interindividual variability in resource use. A major problem in focusing on the feeding behavior of primates is visibility (Clutton-Brock, 1977b). Because of the study troop's semi-terrestriality and because they inhabited a more open environment, it was possible to do a concentrated, longterm, and quantitative study of their feeding behavior. Furthermore, because ringtailed lemurs breed seasonally (van Horn, 1975; Bogart, et al, 1977; Rasmussen, 1985), the effects of the mating period and specific reproductive events on interindividual feeding behavior could be evaluated. Females in a troop were either pregnant or lactating simultaneously, but some females lost their infants early on which allowed a comparison of reproducing and nonreproducing females with environmental factors held constant.

Body size dimorphism has confounded attempts to interpret sex differences in feeding among primates because it is difficult to separate the effects of body size from that of reproductive state. Ringtailed lemurs have limited body size dimorphism (females = 2.50 kg, males = 2.90 kg.; Harvey, et al, 1987), thus the role of reproductive state in creating sex differences in feeding behavior could be clarified. Furthermore, because *L. catta* group members exhibit clear dominance hierarchies (Taylor, 1986) the effect of social factors on interindividual feeding behavior could be measured.

SPECIFIC GOALS AND QUESTIONS

The goal of this project was to examine, in depth, the diet and feeding behavior of adult *L. catta*. This in turn allowed a number of important questions about interindividual differences in feeding ecology to be addressed.

1) Do feeding strategies vary between individuals in any predictable way? Specifically, how do factors such as social status, reproductive state, and gender explain the feeding variations seen? Will reproducing females vary their behavior depending on reproductive state? How will environmental constraints such as food availability affect the feeding behavior of females who will be pregnant during the dry season? Will lactating females increase their intake of protein-rich foods (e.g. young leaves, insects) as has been indicated by some studies (Gautier-Hion, 1980; Harrison, 1983b)?

2) Does high rank result in greater food intake and/or will priority of access to food be correlated with other feeding behaviors such as feeding on clumped versus distributed foods? Will members of the same classes avoid one another during feeding, since their reproductive requirements would be expected to be most similar and competition between them greatest (Robinson, 1981)?

3) Is there behavioral evidence that the uniqueness of female dominance over males among several diurnal polygamous lemur species (*Propithecus verreauxi*, Richard, 1977; *Lemur catta*, Jolly, 1966; Taylor, 1986) is tied to a

variability in resource abundance, as has been suggested by Pollock (1977) and by female reproductive costs, as suggested by Young et al. (1990)?

4) Do different troops within the same reserve differ in their feeding ecology in any way? How does troop size affect foraging behavior?

Early studies of primate feeding ecology focused on interspecific comparisons to identify mechanisms responsible for feeding variation (for example, see papers in Clutton-Brock, 1977a). but such studies were limited due to the difficulty in separating effects of phylogeny from effects of different environmental constraints (see review by Terborgh and Janson, 1986). Intraspecific studies of populations living in different environments were important in helping to separate conservative qualities common to a species from variability created as a result of different environments.

At a finer level, populations are made up of members which belong to different categories such as male, female, pregnant and lactating. Individuals in these categories may have different feeding abilities and nutritional requirements. Focusing on these categories, which are common to most groups, makes it possible to address variation in the feeding ecology of a population based not only on environmental differences, but also upon individual dietary needs. Furthermore, since female reproductive success is more tied to environmental resources, clarifying female foraging behavior will help address how the interplay between female reproductive state, changing nutritional requirements and feeding behavior have influenced the evolution of female foraging strategies and social organization. Given this, demographic parameters such as the number of reproducing females in a population should be expected to affect that group's feeding ecology.

While primate feeding ecology has received considerable attention, only a handful of recent studies have sought to document the effect of any of these factors on basic ecological and social variables (e.g. Stanford, 1989, Barton, 1989). At present we lack a basic understanding of how interindividual variability affects feeding behavior in most primate species. My goal in this study is to provide such information for a lemur species, but the behavioral

adaptations should be common to other species as well. Research on interindividual feeding variability thus complements inter- and intraspecific analyses, and helps to address how the relationship between environmental resources and the abilities and requirements of individuals influence primate ecology and evolution.

In Chapter 2, I describe the research site and methods used. In Chapter 3, I focus on reproductive state, how it affects resource use among females, and how this compares to male feeding behavior. In Chapter 4, the role of social rank in creating interindividual differences in resource use is addressed. In Chapter 5, I compare the feeding and foraging ecology of the two study troops, focusing on group size effects and intergroup resource competition. Chapter 6 includes a description of particular foraging strategies of individuals within a troop. Chapter 7 contains my conclusions. Each chapter includes a theoretical introduction focusing on the specific topic of the chapter.

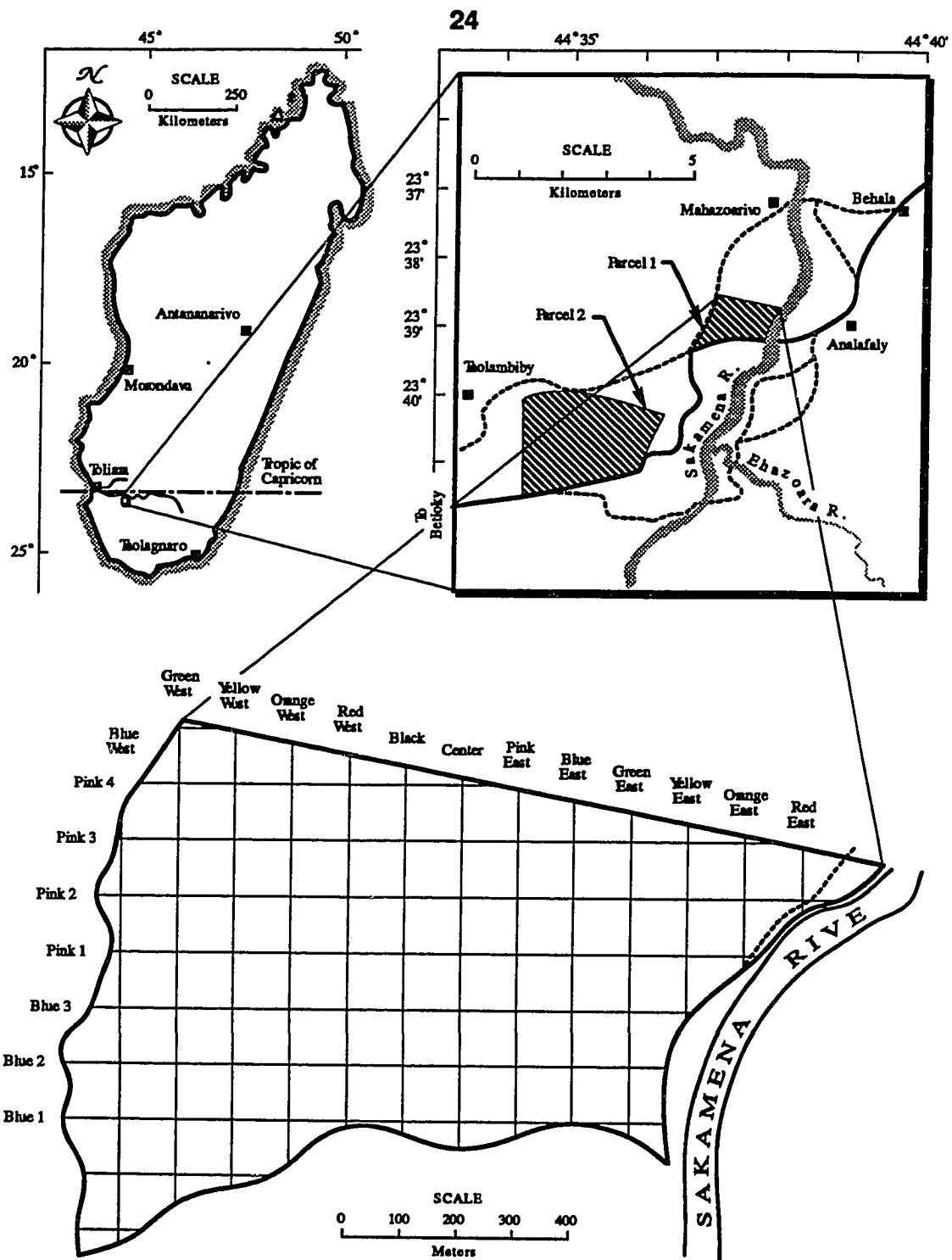
CHAPTER 2

MATERIALS AND METHODS

STUDY SITE

Research was conducted at the Beza Mahafaly Special Reserve, which is located approximately 35 km northeast of the town of Betioky (23° 30'S lat., 44° 40'E long.) (Fig. 2.1 map). This reserve was first established in 1978 and granted special reserve status in 1986. It contains a wealth of birds, mammals, reptiles and insects that are representative of southwestern Madagascar. Hunting does not occur there because of long-standing cultural taboos held by the Mahafaly people who live in this area, and because of the presence of guards. The reserve does contain a natural complement of mammalian and aerial predators, some of which prey on lemurs within the reserve (Ratsirarson, 1985; Sauther, 1989).

In the 13 month study (October 1987 to November 1988), I concentrated on ringtailed lemurs living within an 80 ha fenced and guarded portion of the reserve. The area contains a deciduous and semi-deciduous riverine forest which becomes more xerophytic as one moves from the east to the west. It is dominated by *Tamarindus indica* (commonly known as "kily") in the eastern portion of the reserve, which becomes codominant with *Salvadora augustifolia* and *Euphorbia tirucalli* as one moves to the west. Grazing by sheep and cattle is prohibited, and a rich understorey of herbs and lianas is present. The habitat is very seasonal, with a hot/wet season and a cool/dry season. Based on daily records of temperature and precipitation taken on-site, the mean high for the austral summer at the reserve (October-March) was 37°C., but temperatures could reach 46° C. The mean low during the austral summer was 22°C.. The mean high during the austral winter (April-September) was 32°C. and the mean low was 14°C. Total annual precipitation was 522 mm, and rain fell on 47 days. Rainfall was also seasonal (Fig. 2.2) with 506 mm falling during the austral summer.



Location of Beza Mahafaly Special Reserve

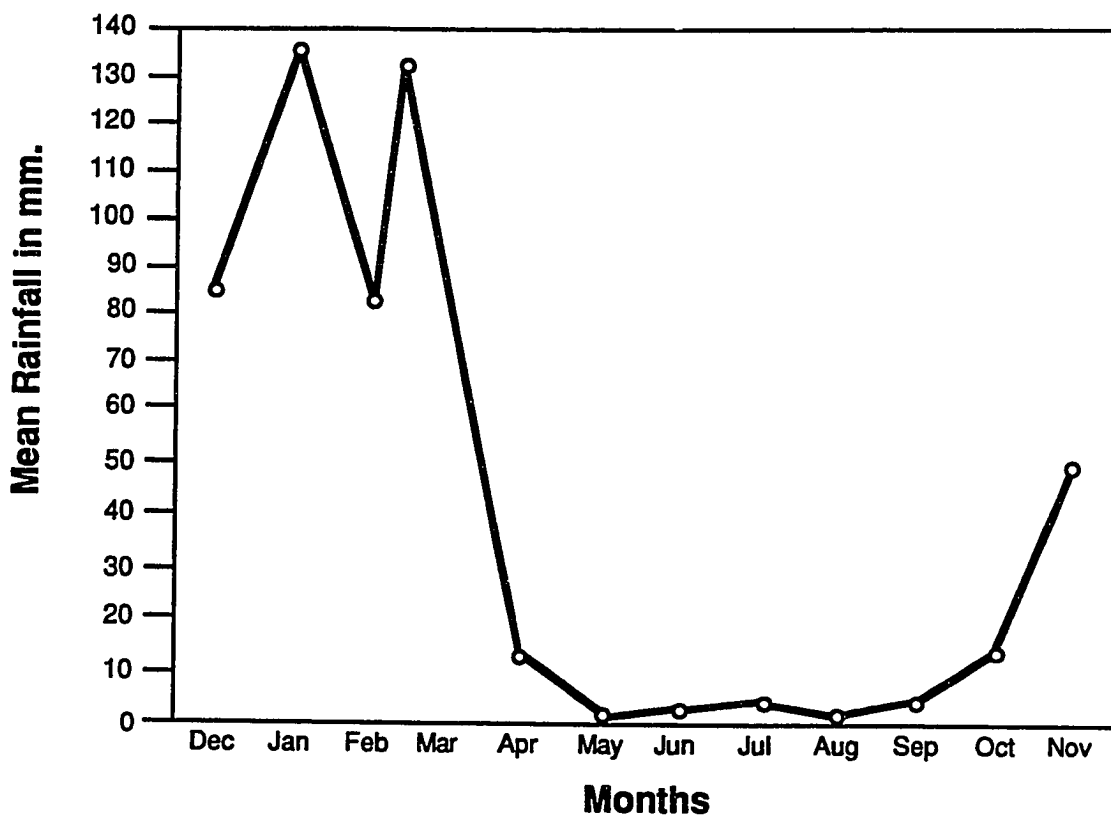


Figure. 2.2 Total Monthly Rainfall at Beza Mahafaly Special Reserve, 1987-1988.

STUDY SUBJECTS

Nine troops of ringtailed lemurs range within the reserve. As a part of a long-term demographic study, all adult females, most adult males and most sub-adult members of these troops have been collared and tagged with a number so that each animal is individually identifiable (see Sussman, 1991). Relative age was based on dental attrition and general physical characteristics of each collared animal.

The study focused on inter-individual variability in the feeding ecology of two *Lemur catta* troops (Black Troop and Green Troop). Members of these troops are presented in Table 2.1. Two adult males in Green Troop were natal

males, as they had been previously tagged and collared as juveniles. Troops were habituated to observers, allowing close range observations (1-2 meters). A total of 16 *L. catta* (7 males and 9 females) were studied, and over 1800h of observations were collected. Preliminary observations began in October, 1987, but the analyses presented here are based on sample periods from December 1987 to November 1988. During the 1987 birth season, the following females gave birth: Green troop, females 13, 33, 53; Black troop, females 02, 82, 42. At this time the other adult females were nulliparous: Green troop, females 93, 73; Black troop, female 62. Females 33 of Green troop and 02 of Black troop lost their infants prior to the beginning of the sample period in December, 1987. There were therefore three nonlactating and two lactating females in Green troop, and two nonlactating and two lactating females in Black troop for comparison. All adult females bred during the mating season in May, 1988. Thus, there were pregnant nine pregnant females for comparison (Green troop: 13, 33, 53, 73, 93; Black troop: 02, 82, 42, 62). Females lactated during the hot wet season (December, 1987 - April, 1988), gestated during the cool dry season (May, 1988 - September, 1988), and gave birth during the transitional period (October - November, 1988). All adult females of Green troop gave birth during the October-November 1988 birth season. In Black troop, one female, 82, lost her infant soon after birth, but the rest still had infants at the end of the study in November, 1988. There were therefore eight females available for comparisons during the transitional birth season. Opportunistic observations of adjacent troops (Red Troop and Blue Troop) were also made. Data were entered directly into hand-held portable computers (Tandy 102: Tandy Corporation, Fort Worth, Texas) powered by solar-rechargeable batteries and were stored on 3 1/2 " computer diskettes.

Table 2.1 Group Composition of Green and Black Troop in May, 1988.

	Green Troop		Black Troop	
	Individual	Rank	Individual	Rank
Adult Females	13	1	02	1
	33	2	82	2
	53	3	42	3
	73	4	62	4
	93	5		
Adult Males	10 ¹	1	99 ¹	1
	30	2	19	2
	50 ³	3	TNT ²	
	86 ³	4		
	70 ⁴			
	60 ⁵			
	23 ⁶			
Juveniles ⁷	one female one male		one male	
Infants	one female (born 10/87) one male (born 10/87)		one female (born 10/87) one male (born 10/87)	

¹ Central Male.

² A 3 1/2 year old natal male from adjacent Blue Troop. He remained with Black Troop from April, 1988 to May, 1988, successfully mated with three Black Troop females, and then returned to Blue Troop.

³ Natal males, each 2 1/2 years old. These males were initially collared and tagged at age 18 months by R.W. Sussman.

⁴ Peripheral male of Green Troop. Only one agonistic episode was recorded between this male and male 86, and none between 70 and 50. Male 70 did clearly rank below 10 and 30, however.

⁵ Transferring male. He successfully mated with two of Green Troop's females, but eventually transferred into adjacent Blue Troop.

⁶ A 3 1/2 year old natal male from adjacent Blue Troop. This male periodically visited Green Troop throughout the year, and successfully mated with female 33, but he remained a member of Blue Troop.

⁷ All juveniles were 18 months old.

BEHAVIORS 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 behaviors except agonism were sampled at five minute intervals. Agonistic behavior was recorded *ad libitum*, even if it did not involve the focal animal. For all behaviors the animal's location was noted. If the behavior was feeding or foraging the species and part used was also recorded. In this study feeding was strictly defined as actual ingestion of food items and does not include handling time. When it could be determined (i.e. for fruits which show a color change associated with ripeness) fruit ripeness was recorded. Handling of and searching for food items is defined as foraging. Fruit foraging involved searching for acceptable fruit based on some quality (most probably ripeness); foraging for leaves involved either attempting to locate leaf buds or young leaves over mature leaves (wet season), or trying to find mature leaves that were not completely dried and dead (dry season). All plant foods used by the two troops were collected and dried for subsequent identification.

At fifteen minute intervals the behavior and location of the focal animal's nearest neighbor, and the observer's location in the forest was recorded. The behavior of each adult member was sampled one day per month for at least 7h by me and my research assistant (Jeff Kaufmann). Each observation day we individually followed a single adult member, therefore two subjects always were sampled simultaneously. Continuous daily observations of both troops by me and my research assistant were made during the mating season, (the month of May) and during the birth season (from late September through early November).

SAMPLE PERIODS

This is a strictly seasonal breeding species (Jolly, 1966, 1967; Van Horn, 1975; Sauther, 1991). It was thus possible to compare lactating and

nonlactating females with environmental factors held constant. In this study lactation occurred during the hot wet season (December, 1987-April, 1988). Because the mating season occurred during the month of May, for the May sample females were followed after they had already mated. Continuous daily observations were also made but were analyzed separately (see below).

The birth season (October, 1988-November, 1988) was a transitional period, both in terms of food availability and reproductive state, and was therefore not included in the above analyses. Instead, during the birth season five females were each followed continuously for approximately one week, and each female gave birth during this period. These data are analyzed and presented separately from the wet and dry season samples, and document changes in behavior associated directly with parturition. Similarly, during the mating season (May), continuous daily observations of three females and one male were also made to determine behavioral changes associated with this period. This data set is also analyzed separately.

SOCIAL RANKS AND SOCIAL STRUCTURE

Social ranks are illustrated in Table 2.2 and 2.3. Relative ranks were determined for all fully adult individuals using three measures: approach/retreat, displacement, and winner/loser in agonistic encounters. All three measures yielded the same hierarchies for all fully adult individuals. Table 2.2 shows winners/losers in feeding contexts. Table 2.3 presents agonistic bouts over grooming partners, and sunning and resting sites. Although less agonism occurs in these contexts, the same rank relationships hold. Thus rank was determined based on agonism in both feeding and nonfeeding situations. The top-ranking male in each troop is referred to as the "central male" for these males also spent more time close to and interacting with the main core of females (the alpha female, the second ranked female and their adult daughters) (see Sauther, 1991).

Taylor's (1986) study of semi-free-ranging ringtailed lemurs in an outdoor enclosure noted rapid rank reversals among females of different matriline, specifically during the birth and weaning periods. In addition she observed

numerous cases of alliances between mothers and daughters formed against females of the opposing matriline. In this study only two rank reversals were observed. On one occasion female 93 won over female 73, and on another occasion male 86 won over male 50. Few alliances were observed within the troop. Coalitions between females *were* seen, however, during intergroup encounters where daughters would support agonistic behavior of their mothers in fights with nontroop females. These different observations may be the result of the artificial nature of the social enclosures in the semi-free-ranging groups. Under free-ranging conditions groups can fission (Sussman, 1991), although it is still unknown whether such fissions occur along matriline. The high level of agonism between the two matriline Taylor (1986) studied was similar to that observed at Beza Mahafaly between different troops, suggesting that this troop might have eventually fissioned along the two matriline had they been a free-ranging group.

The social structure of ringtailed lemurs has been characterized as female dominant (Jolly, 1966; Budnitz and Dainis, 1975; Taylor, 1986; Kappeler, 1989). However, such relationships between individuals are dynamic and may change with age and experience. Nearly all adult females decidedly won over males in all agonistic interactions, but there was one exception in that male 86 won a majority of agonistic interactions with female 93. Both were young adults, and 86 was a natal male who eventually transferred out of the reserve. Furthermore, unlike older adult females, who won all agonistic interactions with all males, the young adult females (73 and 93 and 62) did decidedly lose a few of these encounters to males. It is apparent that in this species female dominance is gradually established and appears to become stable after the female's first mating season (Sauther, 1991).

Table 2.2. Winners and losers of agonistic interactions over food in Green and Black Troop during 1987-1988.

BLACK TROOP

		LOSER							
		Females				Males		Total	
		02	82	42	62	99	19		
WINNER	Females	02	-	13	48	80	38	35	214
	82	0	-	30	54	20	10		114
	42	0	0	-	6	9	10		25
	62	0	0	0	-	5	4		9
Males	99	0	0	0	5	-	32		37
	19	0	0	0	4	0	-		4
Total		0	13	86	149	72	91		

GREEN TROOP

		LOSER															
		Females					Males										
		13	33	53	73	93	10	30	50	86	70	60 ¹	20 ¹	23 ²	38 ²	Total	
WINNER	Females	13	-	45	89	61	26	49	19	28	49	12	3	-	-	-	381
	33	0	-	26	21	18	36	14	28	8	6	1	-	-	-	158	
	53	0	0	-	21	36	33	24	21	21	21	13	5	-	-	195	
	73	0	0	0	-	11	17	3	10	12	1	0	-	-	-	45	
	93	0	0	0	1	-	23	8	21	6	10	4	1	-	-	73	
Males	10	0	0	0	2	4	-	12	9	23	9	3	1	2	-	65	
	30	0	0	0	1	2	0	-	1	2	10	2	0	0	2	20	
	50	0	0	0	2	3	0	0	-	12	0	1	3	0	0	21	
	86	0	0	0	8	8	0	0	1	-	1	0	1	0	1	20	
	70	0	0	0	0	0	0	0	0	0	-	0	4	1	0	5	
	60 ¹	0	0	0	0	0	0	0	0	0	0	-	0	0		0	
	20 ¹	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	
	23 ²	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	
	38 ²	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	
Total		0	45	115	117	107	158	80	119	133	60	27	14	3	2		

¹ Males which attempted to transfer into Green Troop.

² Males of adjacent troops who periodically visited Green Troop.

Table 2.3. Winners and losers of agonistic interactions over non-feeding contexts in Green and Black Troop during 1987-1988.

BLACK TROOP

LOSER

		Females				Males		Total	
		02	82	42	62	99	19		
WINNER	Females	02	-	15	55	92	47	38	247
	82	0	-	35	57	25	11	128	
	42	0	0	-	7	12	11	30	
	62	0	0	0	-	6	5	11	
	Males	99	0	0	0	5	-	36	41
19	0	0	0	4	0	-	4		
Total		0	15	90	165	90	101		

GREEN TROOP

LOSER

		Females					Males										Total
		13	33	53	73	93	10	30	50	86	70	60**	20**	23*	38*		
WINNER	Females	13	-	47	97	63	28	52	24	30	50	13	4	-	-	-	404
	33	0	-	32	24	19	37	15	29	9	8	4	-	-	-	173	
	53	0	0	-	29	44	42	27	23	31	23	14	8	-	-	227	
	73	0	0	0	-	12	18	5	13	16	2	0	-	-	-	66	
	93	0	0	0	1	-	24	10	24	3	10	6	1	-	-	73	
Males	10	0	0	0	2	4	-	13	12	24	10	4	4	2	-	71	
	30	0	0	0	1	2	0	-	1	2	11	3	4	0	2	23	
	50	0	0	0	2	3	0	0	-	12	0	1	3	0	0	20	
	86	0	0	0	8	8	0	0	1	-	1	0	1	0	1	20	
	70	0	0	0	0	0	0	0	0	0	-	0	5	1	0	6	
	60**	0	0	0	0	0	0	0	0	0	0	-	0	0		0	
	20**	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	
	23*	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	
	38*	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	
Total		0	47	129	130	120	173	94	133	147	78	30	26	3	2		

** Males which attempted to transfer into Green Troop.

* Males of adjacent troops who periodically visited Green Troop.

STATISTICAL METHODS

A common limitation in the study of animal behavior is that often the same individuals are sampled repeatedly, and thus the samples lack both randomness and independence. Furthermore, sample sizes are often relatively small. Because of this, nonparametric methods are often used to analyze such data (Thomas, 1986). However, many nonparametric methods lack efficiency, and information is lost (Thomas, 1986), especially if one's data set contains interval data. Furthermore, nonparametric tests make the specific assumption that the sample being analyzed was produced through random sampling which, as noted above, is often not a valid assumption in behavioral studies (Sussman, et al. 1979). An increasingly accepted method for the analysis of such data is the use of randomization tests, which results in a distribution-free test (Edgington, 1980; Manly, 1991). The concept of such tests is very old, but before the advent of computers such an approach was not practical. As Manly (1991, p. 17) has pointed out "classical tests can be thought of as approximations for randomization tests".

A randomization test compares results obtained with results generated by randomly re-ordering the data. For example, one of the foci of this study was to determine interindividual variability in feeding. Mean weights of fruits ingested by males and pregnant females were obtained (males: $\bar{x} = .03$ grams fruit; pregnant females: $\bar{x} = .36$ grams fruit). The question then became, were the differences between these means significantly different or simply due to chance? Using a portable computer with a random generator program (adapted from a program by Dr. James Cheverud and Dr. Malcolm Dow), the original data set was reordered at least 1000 times. Each time this occurred the computer kept a running count of the mean differences obtained in this random manner. These results are illustrated in Fig. 2.3. Based on the original data set, of the permutations generated by the computer the observed mean difference of .33 grams occurred in only 1 out of 1000, which gives a significance level of $1/1000 = .001$. Such a result is a good indicator that males and pregnant females differ in their use of fruit. In this study, therefore, a t test with systematic data permutation was used to test for statistically

significant differences between individuals of varying reproductive states and social ranks, or between different troops. I employed 1000 random permutations to generate a *t* statistic, but when results were nearly significant I repeated the analysis with 5000 random permutations to guard against type II errors (Manly, 1991). For this study significance was set at .05. Frequency data were obtained using the SAS statistical package (SAS Institute, Cary, NC). All other data were analyzed using a Macintosh Plus computer (Apple Computer, Inc., Cupertino, California) and the QuickBasic application (Microsoft Corporation, Redmond, Washington). Correlation coefficients were also generated for some data sets and analyzed using the Statview II application (Abacus Concepts, Berkeley, California).

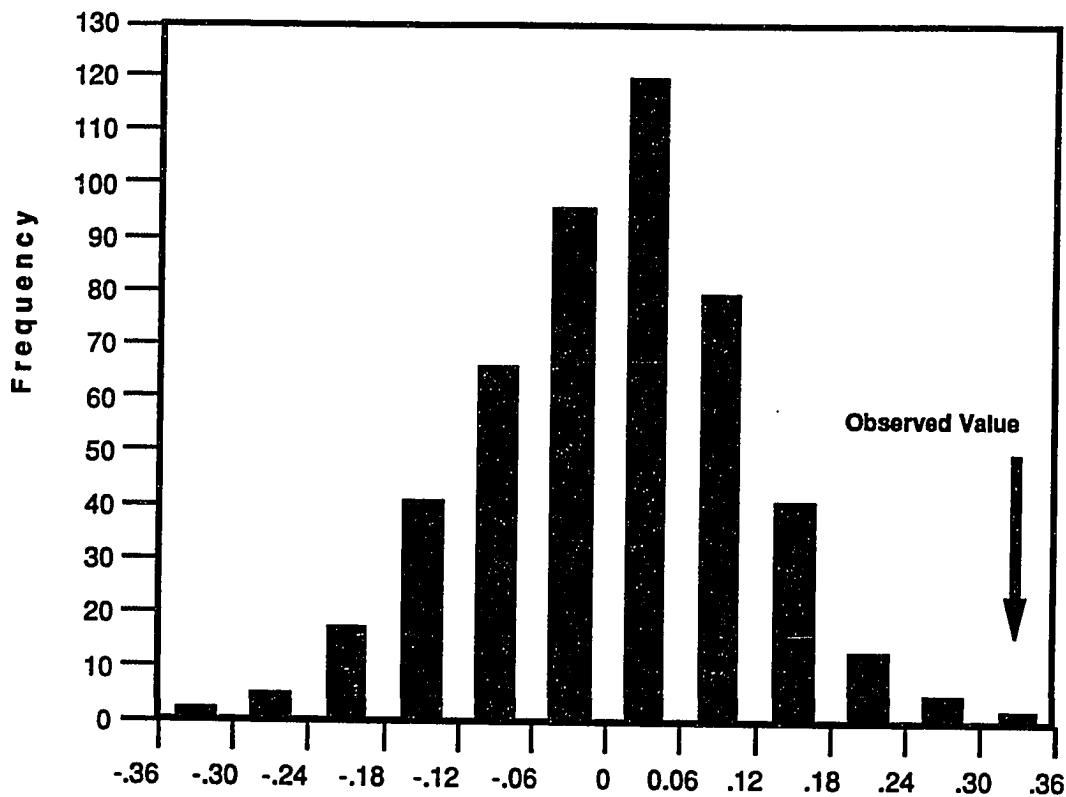


Figure 2.3 . Results of Randomization of Mean Differences (Males - Females) in Fruit Intake in Grams

PHENOLOGY

The phenology of 119 trees and 31 species were monitored monthly. Within each troop's home range, all trees located along 6 separate ha of trails were monitored. These ha were distributed randomly within each home range. Each phenological sample was made the day just prior to the start of the monthly observations for the troops. From the phenological samples it is clear that food availability during the wet season was greater than during the dry season (Fig 2.4). During the dry season both fruits and leaves became rare (Fig. 2.5). Of the fruits utilized by the study troops only two species were available throughout the dry season. These were *T. indica* and *Enterospermum pruinosa* (Fig. 2.5). During the latter part of the dry season (August-September) the availability of both young and mature leaves was reduced, and individuals were often observed ingesting completely dried brown leaves. Flowers, however, became more abundant from September - October.

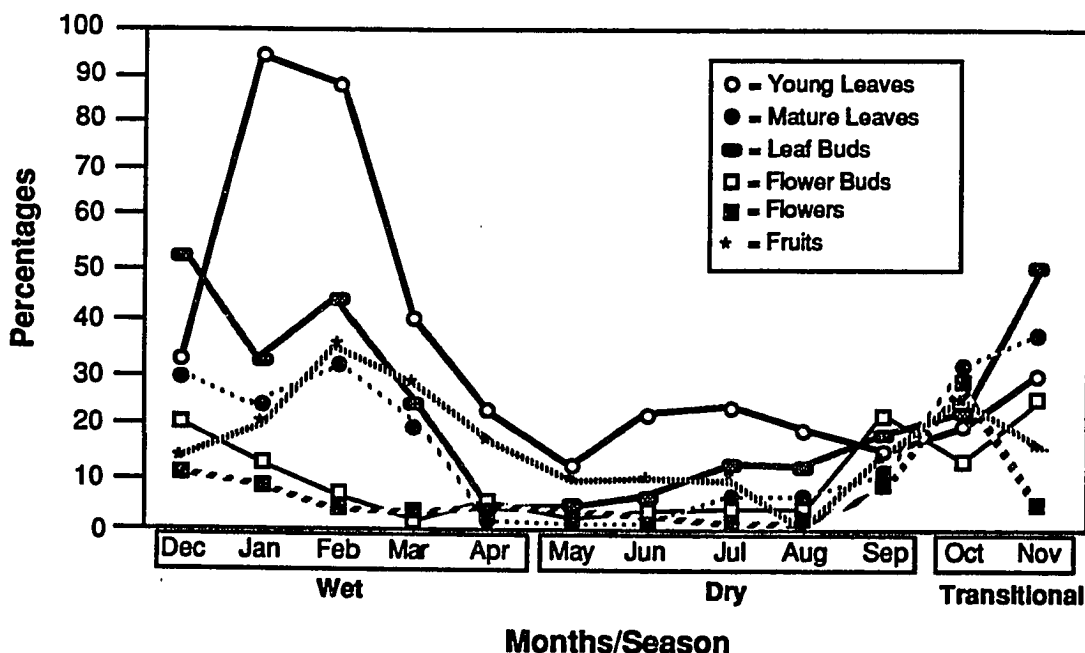


Figure 2.4. Monthly Percentage of Phenology Trees Exhibiting the Presence of Plant Parts

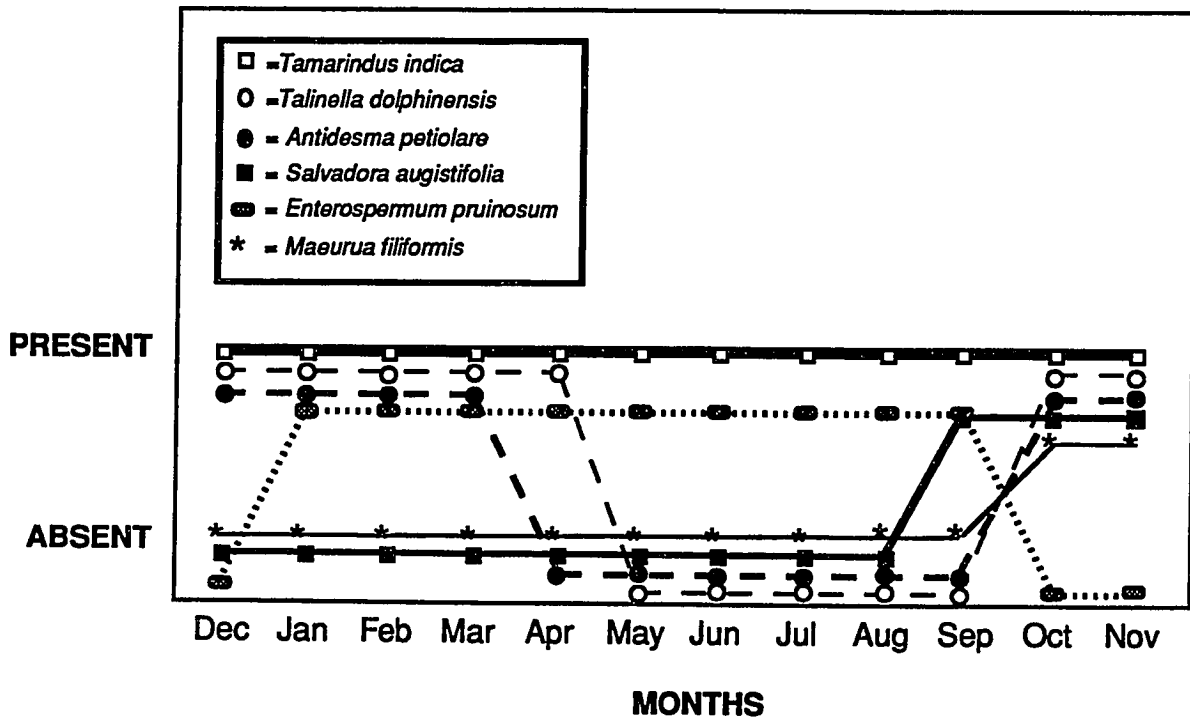


Figure 2.5 Fruit Availability based on Phenological Samples
***L. CATT* PLANT FOODS**

Plant foods used as food by ringtailed lemurs during the study period are listed in Table 2.4. *L. catta* used a total of 62 species. Of these, 29 species were used for fruits, 38 species for leaves, and 19 species for flowers. Green Troop used a total of 50 species while Black troop used a total of 44 species.

Table 2.4. *Lemur catta* foods.

Text Abbreviation	Family	Genus	Species	Part ¹	Troop ²
8B	MALVACEAE	<i>Abutilon</i>	<i>pseudocleistogamum</i>	LV	B
AB	FABACEAE	<i>Abrus</i>	<i>precatorius</i>	LV	B
AC	MIMOCACEAE	<i>Acacia</i>	<i>sp.</i>	LV	G/B
1H	EUPHORBIACEAE	<i>Acalypha</i>	<i>sp.</i>	FL/LV	G
AA	AMARANTHACEAE	<i>Achryanthes</i>	<i>aspera</i>	LV	G
AS	PASSIFLORACEAE	<i>Adenia</i>	<i>sphaerocarpa</i>	LV	G
AP	EUPHORBIACEAE	<i>Antidesma</i>	<i>petiolare</i>	FR	G/B
6G	PAPAVACEAE	<i>Argemone</i>	<i>mexicana</i>	FL/LV/ST	G/B
2C	ARISTOLOCHACEAE	<i>Aristolochia</i>	<i>aurita</i>	LV	G/B
AT	SALVADORACEAE	<i>Azima</i>	<i>tetracantha</i>	FR	G/B
6D	COMPOSITAE	<i>Bidens</i>	<i>sp.</i>	LV	G
BV	STERCULIACEAE	<i>Byttneria</i>	<i>voulily</i>	LV	G/B
CC	CAPPARIDACEAE	<i>Capparis</i>	<i>chrysameia</i>	FR/LV	G/B/R
BE	RUBIACEAE	<i>Catunaregam</i>	<i>spinosa</i>	FR	G/B
GG	MELIACEAE	<i>Cedrelopsis</i>	<i>grevei</i>	FR/FL/LV	G/B/R
1G	VITACEAE	<i>Cissus</i>	<i>microdonta</i>	FR	G/B
OD	VERBENACEAE	<i>Clerodendrum</i>	<i>sp.</i>	LV	G
2F	NYCTAGINACEAE	<i>Commicarpus</i>	<i>commersonii</i>	LV	G/B/R
CO	COMBRETACEAE	<i>Combretum</i>	<i>sp.</i>	LV	R
CL	CUCURBITACEAE	<i>Corallocarpus</i>	<i>grevei</i>	FR/LV	G/B
CE	CAPPARIDACEAE	<i>Crateva</i>	<i>excelsa</i>	FL/LV	G/B
8E	FABACEAE	<i>Crotalaria</i>	<i>sp.</i>	FL/LV	G
ON	ASCLEPIADACEAE	<i>Cynanchum</i>	<i>nodosum</i>	FR/FL	B
ES	RUBIACEAE	<i>Enterospermum</i>	<i>pruinsum</i>	FR	G/B/R
EU	EUPHORBIACEAE	<i>Euphorbia</i>	<i>tiricalli</i>	ST	G
FM	BIGNONIACEAE	<i>Fernandoa</i>	<i>madagascariensis</i>	LV	G/R/B
2G	FLACOURTIACEAE	<i>Flacourtia</i>	<i>ramontchi</i>	FR	B
5C	EUPHORBIACEAE	<i>Fluggea</i>	<i>sp.</i>	LV	G/B
GL	LILIACEAE	<i>Gloriosa</i>	<i>superba</i>	FL/ST/LV	G/B
4E	RHAMNACEAE	<i>Gouania</i>	<i>sp.</i>	LV	G/B
03	TILIACEAE	<i>Grewia</i>	<i>clavata</i>	FR/FL	G/B
G2	TILIACEAE	<i>Grewia</i>	<i>humbertii</i>	FR	G
GG	TILIACEAE	<i>Grewia</i>	<i>greveii</i>	FR/FL/LV	G/B

Text Abbreviation	Family	Genus	Species	Part	Troop
G6	TILIACEAE	<i>Grewia</i>	<i>leucophylla</i>	FR	G
G4	TILIACEAE	<i>Grewia</i>	<i>triflora</i>	FR/LV	G/B
1C	TILIACEAE	<i>Grewia</i>	<i>sp.</i>	FR	G
GA	HERNANDIACEAE	<i>Gyrocarpus</i>	<i>americanus</i>	FL/LV	G/B
MC	CONVOLVULACEAE	<i>Hildebrandtia</i>	<i>sp.</i>	LV	G/B
H2	CELASTRACEAE	<i>Hippocratea</i>	<i>sp.</i>	LV	G/B
5G	CONVOLVULACEAE	<i>Ipomoea</i>	<i>cairica</i>	FL/LV	G
7C	ACANTHACEAE	<i>Justicia</i>	<i>glabra</i>	LV	G/B
3G	FABACEAE	<i>Lablab</i>	<i>boivinii</i>	FR/LV	G
3D	ORCHIDACEAE	<i>Eulophia</i>	<i>sp.</i>	FL	G
MF	CAPPARIDACEAE	<i>Maurua</i>	<i>filiformis</i>	FR/FL/LV	G/B
4D	CAPPARIDACEAE	<i>Maurua</i>	<i>mida</i>	FR	G
PE	ASCLEPIADACEAE	<i>Marsdenia</i>	<i>sp.</i>	FR/FL/LV/ST	G/B
7G	CELASTRACEAE	<i>Maytenus</i>	<i>linearis</i>	FL	G/B
6A	CONVOLVULACEAE	<i>Metaporana</i>	<i>parvifolia</i>	LV	G/B
ND	OLEACEAE	<i>Noronhia</i>	<i>sp.</i>	FR	R
3B	OLACACEAE	<i>Olex</i>	<i>androyensis</i>	FR	G/B
4F	RUBIACEAE	<i>Paederia</i>	<i>grandidieri</i>	LV	G/B
PS	CAPPARIDACEAE	<i>Physena</i>	<i>sessiflora</i>	FR	G
QJ	MELIACEAE	<i>Quisivianthe</i>	<i>papinae</i>	FL	G/B
9C	FABACEAE	<i>Rhynchosia</i>	<i>sp.</i>	LV	G/B
6C	ACANTHACEAE	<i>Reullia</i>	<i>anaticollis</i>	LV	G/B
SA	SALVADORACEAE	<i>Salvadora</i>	<i>augistifolia</i>	FR/FL/LV	G/B
SM	RHAMNACEAE	<i>Scutia</i>	<i>myrtina</i>	FR	G/B/R
H1	ASCLEPIADACEAE	<i>Secamone</i>	<i>sp.</i>	LF	G/B/R
SE	CUCURBITACEAE	<i>Seyrigia</i>	<i>sp.</i>	FR	G
TA	PORTULACACEAE	<i>Talinella</i>	<i>dolphinensis</i>	FR/LV/ST	G/B
TI	CESALPINIACEAE	<i>Tamarindus</i>	<i>indica</i>	FR/FL/LV	G/B/R
4C	VERBENACEAE	<i>Vitex</i>	<i>sp.</i>	FR	G/B

¹ FR = FRUIT; FL = FLOWER; LF = LEAVES; ST = STALKS.

² G= GREEN TROOP; B = BLACK TROOP; R = RED TROOP.

FEEDING BEHAVIOR OF LEMUR CATTAL AT BEZA MAHAFALY SPECIAL RESERVE.

Food availability at the reserve varied throughout the year. *L. catta* at Beza Mahafaly were able to rapidly switch their dietary focus as new foods became available, and they often made long "excursions" out of their normal home range to monitor seasonal food sources. In the wet season foods were more abundant, but during the dry season both fruits and leaves became less available (Fig. 2.4). Most individuals adapted to this period by eating fewer species of leaves and fruits, including less palatable food items such as mature leaves and spiny weed species (e.g. *Argemone mexicana*) in their diets, searching out patchily distributed fruits of *T. indica* (often feeding on drier pods which had fallen to the ground), reducing overall activity and by resting more. Leaves of herbaceous species and deciduous trees were selected, but some evergreen species were used as well. Flowers became available, especially during September and October when large trees produced abundant flowers (e.g. *Quivisianthe papionae*; *Gyrocarpus americanus*).

The ringtailed lemurs were opportunistic feeders with a wide dietary regime that included fruits, leaves, leaf stems, flowers, flower stems, spiders, spider webs, caterpillars, cicada, and insect cocoons. In addition, on one occasion female 33 of Green Troop attempted to catch an unidentified bird which then flew into the bushes. Termite mounds built either on the ground or inside rotting trees were also plentiful in the forest and at least once daily, troop members would either lick, or less often ingest the soil from the mounds or the trails of digested cellulose left behind by the termites. They were never observed actually eating termites, per se, only licking or ingesting the trails or soil from the mounds. O'Connor (1987), however, mentions termite eating. She also reports seeing ringtailed lemurs at Berenty eating small quantities of dead wood. This was not observed at Beza Mahafaly, but individuals would lick termite trails inside of and on the surface of dead wood. O'Connor saw soil ingestion, but it is unclear if this was from termite mounds.

L. catta are highly synchronous in their activities. All individuals feed at the same time when there is ample food. If a resource is limited, e.g. a single drinking site, individuals may queue up for access to such items. Infants often smell or taste food in their mother's mouth, and individual adults commonly smell each other's mouths, perhaps to monitor available food sources.

Ringtailed lemurs display a more limited dexterity in the handling of food items when compared to anthropoid primates. Food items are not manually manipulated, but rather are simply grasped and held. Most food is eaten by mouth, one item at a time, directly from the source. Food items on branches (e.g. fruit, leaf buds) are brought to the mouth by the individual grasping the branch and pulling the food item nearer to the mouth. Fruit is rarely processed using the incisors. Either the whole fruit is put into the mouth and chewed, or for larger fruits such as *T. indica* the fruit is held by hand, inserted into the side of the mouth and processed using the molars.

At Beza Mahafaly, as elsewhere, *L. catta* spends a fair amount of time feeding on the ground (Green Troop = 18%; Black Troop = 20%). Items eaten at this level are primarily the leaves of herbaceous species, termite soil, and the fruit of *T. indica*, which periodically ripen and fall to the ground.

DESCRIPTION OF METHODS FOR DETERMINING FEEDING BEHAVIOR

Hladik (1977a) has discussed the potential limitations in using time spent feeding as a measure of food intake. For example, he showed that free-ranging chimpanzees (*Pan troglodytes*) spent 14% of their time feeding on fruits, but in terms of weight (based on collecting and weighing the number of food items actually ingested) fruit made up 62.2% of their diet. However, counting, collecting and weighing the actual number of food items eaten is less feasible for highly arboreal species where observations are often limited. Even under the best of observation conditions it can be extremely fatiguing to rapidly identify and count every food item ingested (Sauther, 1984). Furthermore, when food items are small and roughly similar in size, there is

a fair correspondence between time spent feeding and estimates of amounts ingested (Hladik, 1977b,c; Sauther, unpublished data). Of the identified food items in the ringtailed lemur diet, only one species, *T. indica*, was too large for the lemurs to place the entire item into the mouth and chew. All other foods were of a small and roughly uniform size, and all of these foods were picked by the mouth, one part at a time, directly from the source. Thus leaves, leaf buds, flowers and all fruits (except *T. indica* and *Catanaregam spinosa*) were plucked, singly, by the mouth and consumed. For this study, a combination of time spent feeding and Hladik's collection method was therefore employed and is described below.

Because ringtailed lemurs are semi-terrestrial, observation of feeding behavior was excellent. Only a small percentage of feeding bouts during the five minute samples was missed due to the subject being out of sight to the observers. These occurred during the first two preliminary weeks of observation and are not included in the analyses.

Single food items (individual bites in the case of *T. indica* fruit) were ingested one at a time, thus each five minute sample spent feeding on these foods is a reflection of the consumption of a least one food item of that species and part.

Major plant food species were collected and both fresh weight and dry weight of a single food item were determined based on the mean weight of 100 representative samples (Hladik, 1977b). Plant foods were collected the day after the last pair of subjects had been followed. For these food species an estimation of food intake was made by multiplying the total number of five minute samples the subject fed on that species and part (with each five minute sample representing the ingestion of one such food item) by the mean wet weight for that species and part. This is expressed by the following formula:

$$E_x = \sum_{i=1}^n x_i * W_x$$

where x = the number of five minute samples the focal animal fed on species and part x , W_x = wet weight of a single species and part x , and E_x = estimate of amount ingested of species and part x . This provides, for each subject, the estimated *minimum* weight of a particular species and part actually ingested. However, for such estimations to be valid, bite rates of these foods between individuals must not be significantly different. Bite rates for particular food items were determined by recording the number of food items ingested per second. The average bite rate for particular species and parts is given in Table 2.5. There were no significant differences between individuals for bites rates on these foods. Furthermore, the mean bite rates for the same species and parts were strikingly similar for each troop (Table 2.5). Therefore, when individuals or classes of individuals (e.g. lactating versus males), or groups fed on these particular species and parts the minimal weights ingested are compared.

Table 2.5. Bite Rates for particular foods for individuals in Green and Black Troop.

GREEN TROOP

Foods

Subject	QUFL*	G6FR	MCYL	03FR	TAFR
13	.57	.30	.37	.36	.35
33	.57	.30	.42	.36	.34
53	.47	.32	.45	.37	.40
73	.55	.28	.38	.31	.37
93	.58	.27	.43	.33	.37
10	.54	.26	.43	.33	.36
30	.46	.32	.37	.33	.36
50	.48	.27	.37	.30	.39
86	.50	.27	.43	.33	.41
70	.55	.25	.40	.31	.40
$\bar{x}$	.53	.28	.41	.33	.38

* See table 2.4 for a list of abbreviations for foods.

BLACK TROOP

Foods

Subject	QUFL*	APFR	03FR	TAFR
02	.60	.42	.36	.38
82	.52	.41	.34	.35
42	.50	.36	.30	.37
62	.57	.38	.31	.41
99	.57	.38	.30	.39
19	.50	.43	.33	.40
$\bar{x}$	.54	.40	.32	.38

A slightly different method was used when comparing the use of the fruits of *T. indica*. When feeding on this fruit the pod would be held in one hand, and the lemur would place the tip into the side of the mouth and crack and remove the hard covering. The individual would then lick the fruit until a single seed with its surrounding flesh could be bitten off. The seed and covering were then swallowed whole. An individual was scored as feeding on kily only if a seed had been ingested. Otherwise it was scored as "licking".

A cross-section of a kily pod is shown in Fig. 2.6 showing the individual seed in the pod. Ringtailed lemurs pass the seeds of *T. indica* without digesting them. To determine the weight of kily ingested, the fruits were cut into separate seeds with the surrounding flesh, the seeds were removed, and the mean weights were then based on 100 counts of the outside flesh. The other species held in the hand, *Catanaregam spinosa* was not ingested. This fruit was broken open and the juicy interior was then licked.

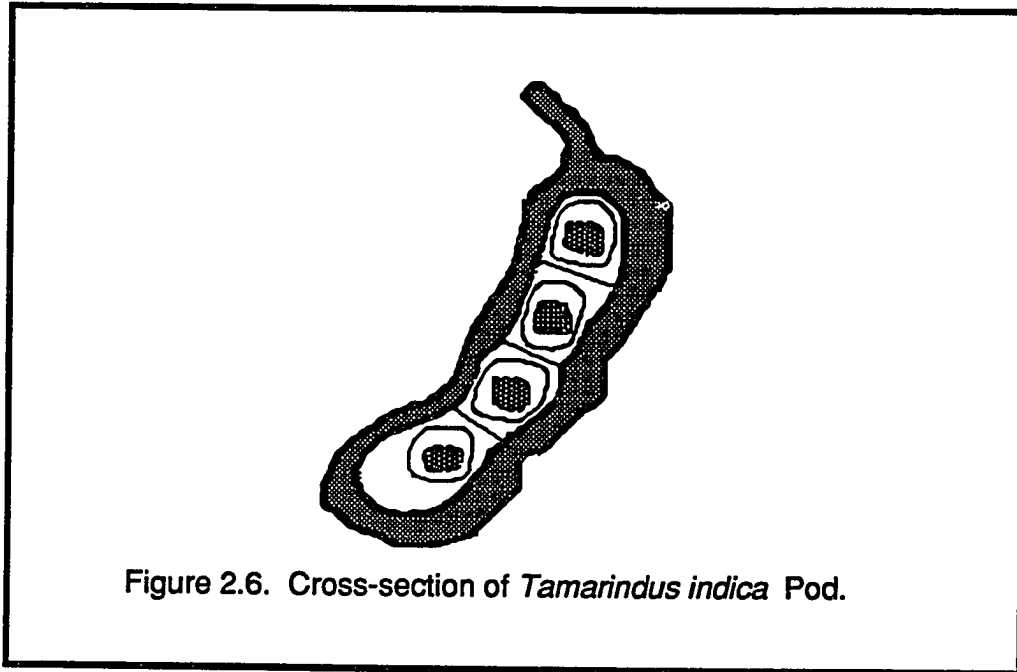


Figure 2.6. Cross-section of *Tamarindus indica* Pod.

Each individual was sampled one full day per month, and these months were then grouped into wet, dry and transitional seasons based on rainfall and phenology. The wet and dry seasons were each five months long, and the transitional season was two months. For most analyses the unit of comparison was the proportion of time or, for food, the minimum weight ingested per season. When I compared food parts, e.g. fruits, leaves, flowers, I took the top 20 foods ingested by each individual (based on total minimum weights for the year or for the season). For example, leaf feeding during the wet season by female 13 was based on the total minimum weight of leaves she fed on each month of the wet season (determined by the formula above) averaged over five months, the length of the wet season (December, 1987-

April, 1988). Thus it would be the total minimum weight divided by five. Since most foods were very seasonal and were utilized for only a few months of the year, a slightly different method was used to determine mean weights for particular species and parts of foods. In these cases, the weights were determined per hour, (based on the number of five minute samples per hour that the individual fed on that particular food) and then averaged by the total number of hours an animal spent feeding when such foods were phenologically available. Thus if female 13 fed on leaf buds of *T. indica* three times from 6 to 7 am, four times from 8 to 9 AM, and three times from 4 to 5 PM, and the weight of a single leaf bud was = 0.03 grams, then for that day she ingested a minimum total weight of 0.30 grams of leaf buds. During the period that leaf buds were available, she was scored as feeding during 10 hours. Her mean intake would be thus be 0.30 divided by 10 = 0.03 grams.

CHAPTER 3

REPRODUCTIVE STATE AND RESOURCE USE

INTRODUCTION

BEHAVIORAL ADAPTATIONS ASSOCIATED WITH REPRODUCTION

For most mammals reproduction can be divided into the following discrete events: mating, gestation, parturition, lactation, and maternal recovery. Studies which seek to determine mammalian reproductive costs, especially those involving energetics, have focused on changes associated with specific reproductive states rather than a comparative approach (Gittleman and Thompson, 1988). This is limited from an evolutionary perspective, for without comparative data it is difficult to determine which states are associated with higher foraging and nutritional costs, and hence under stronger selective forces. Furthermore, "behavioral compensation" (Gittleman and Thompson, 1988), as a method of lessening the costs of reproduction, can affect activity budgets, and has not been investigated throughout all reproductive events. Behavioral adaptations associated with reproduction thus include changes in relative activity patterns, as well as foraging and feeding ecology. In this chapter behavioral changes associated with the various reproductive events are presented.

Lactation

It is generally accepted that lactation is a costly reproductive state for placental mammals (Sadleir, 1969; Robbins, 1983; Clutton-Brock et al., 1989), as well as nonplacental mammals (Clarke and Loudon, 1985). Increased food intake has been reported for a whole range of lactating mammals (Wallabies: Clarke and Loudon, 1985; Bats: Studier, et. al. 1973; Bank Voles: Kacsmarski, 1966; Mice: Miller, 1975; Hamsters: Fleming, 1978; Sheep: Hadjipieris and Holmes, 1966; Deer: Sadleir, 1982, Clutton-Brock et al, 1989; Primates: Sauther and Nash, 1986, Roberts, et. al, 1985; Humans: Blackburn and Calloway, 1976). Among primates, captive studies have repeatedly demonstrated this by

plotting food intake in general, or energy intake in particular across different reproductive states. For example, Sauther and Nash (1986) found that for captive galagos (*Galago senegalensis braccatus*) food and energy intake increased throughout lactation, and was greater than during pregnancy. Similar results are reported for cotton-top tamarins (Kirkwood and Underwood, 1984). The same trend occurs for larger primates. Roberts, et. al. (1985) plotted the energy intake of six intact (nonovariectomized) baboons during various reproductive states. At the beginning of lactation, energy intakes were 11% greater than during the nonreproductive, weight - maintaining phase. This increased to a 27% greater intake during the course of lactation.

At Beza Mahafaly females lactated and weaned their infants during the period of food abundance. With the onset of the rains in November, deciduous tree species within the reserve quickly re-foliated, herbaceous and climbing species became abundant, and young leaves and fruits became available (see Fig 2.4). However, there is evidence from this study to suggest that lactating ringtailed females were under considerable nutritional stress. Because of the seasonal nature of ringtailed lemur reproduction, all females were pregnant during the dry season when less food was available (Fig. 2.4). Thus a pregnant female most likely entered lactation with little or no nutrient reserves. Furthermore, lactating *Lemur catta* females exhibited obvious signs of stress. During the course of lactation they visibly lost weight, which is a common pattern among lactating mammals (Sadleir, 1969), and had dull coats relative to males and nonlactating females. Infants of the study troops were still periodically on the nipple by late February/early March and were sporadically carried as late as March. Strepsirhines, including *L. catta* produce smaller neonates relative to body size than haplorhine primates (Jolly, 1984). This means they must support altricial infants during a rapid early growth period. In addition, infant lemurs develop rapidly, (Klopfer, 1974; Sussman, 1977), with active environmental exploration occurring by week two of life and social play beginning by week 6 (Gould, 1990). As such, ringtailed lemur infants would be expected to be relatively costly for a mother to support (King and Murphy, 1985), and lactating ringtailed lemurs should be

expected to exhibit different feeding behaviors when compared with other classes of individuals.

Pregnancy

For mammals in general, pregnancy appears to be a less demanding reproductive state when compared to lactation (Sadleir, 1969; Clutton-Brock et al, 1989). Nevertheless, relative to nonlactating, nonpregnant individuals, increased food intake during pregnancy has been reported for a number of mammals, (Rats, Russell, 1948; Mice: Russell, 1948; Miller, 1975; Bank Voles, Kacsmarski, 1966; Bats, Stones and Weibers, 1965; Sheep: Hadjipieris and Holmes, 1966), but not all (Golden Hamsters: Quek and Trayhurn, 1990). For humans, Blackburn and Calloway (1976) report that pregnant women have a higher energy intake than nonlactating, nonpregnant women. While energy cost associated with pregnancy has been found to increase as the pregnancy progresses (Emerson, et al. 1972), voluntary caloric intake has not been found to increase during pregnancy (Darby et. al., 1953; Beal, 1971). Increased ingestion of some micro-nutrients has also been reported during pregnancy (salt intake: Humans, Brown and Toma, 1986; calcium: Rats, Woodside and Millelire, 1987)

There is little information on food intake by pregnant nonhuman primates, and this is mainly for baboons. Silk (1987a) documented that activities and feeding behavior of free-ranging pregnant baboons changed during pregnancy. Grass corms and especially seeds were more heavily utilized as the baboon's pregnancy progressed. Muruthi et al, (1991) found that free-ranging pregnant baboons (*Papio cynocephalus*) spent more time feeding and had greater daily estimated energy and protein intake than cycling females. In a captive study of cotton-top tamarins, Kirkwood et al. (1984) found no consistent increase in energy intake over the course of pregnancy, and that energy intake during pregnancy did not vary markedly from amounts used when nonpregnant and nonlactating. Kemnitz, et. al, (1984) also report for captive baboons that food intake, in grams, was not higher during pregnancy than during the nonpregnant nonlactating state. Riopelle, et al. (1984) have suggested that metabolic efficiency may increase

during pregnancy and may explain the lack of increased intake for various measures. They found that pregnant rhesus monkeys fed low amounts of high quality protein had a post delivery weight nearly equal to pre-conception, whereas nonpregnant females fed the same percentage of protein lost weight even though they were fed the same Kcal/kg.

Food intake has been reported to actually decrease as parturition nears. Sauther and Nash (1986) found that food intake of pregnant bushbabies (*Galago senegalensis braccatus*), one week prior to parturition, was lower than these same females in a nonpregnant, nonlactating state. Kohrs, et al. (1976) report a 10% decrease in food intake by the 80th day of pregnancy in the rhesus macaque. Both Beal (1971) and Darby, et al, (1953) found a 10% decrease in total caloric intake during the last trimester of human pregnancy. Sucrose consumption in captive baboons has also been reported to increase significantly by the end of the first trimester and then decrease prior to parturition (Kemnitz, et al, 1986).

At Beza Mahafaly, it might seem that pregnant females experienced fewer potential stresses as they entered gestation. As already noted, lactation occurred during the wet season which was a period of relative food abundance. By the end of March, infants rarely nursed, and they moved almost entirely on their own by this time. Thus even lactating females had at least one month during which maternal costs were probably reduced. This is supported by the subjective observation that lactating females rapidly gained weight and improved coat condition by the end of April. However, this is a seasonally breeding species, which bred during the month of May. During both April and May increased activity by both males and females was noted (Sauther, 1991). Specifically, during this period aggressive encounters between different troops heightened (Fig. 3.1). Inter-troop encounters in ringtailed lemurs are characterized by highly aggressive fights between females of different troops, often involving canine slashing, jump fights, and 8 meter falls out of trees. Furthermore, with the drastic drop in rainfall in April (Fig. 2.1) many deciduous tree species lost their leaves, and food availability decreased (Fig. 2.4). As such, it is unlikely that female *L. catta* entered pregnancy with any nutritional advantage. Because pregnancy

occurred during the dry season these females were contending not only with increased demands associated with pregnancy, but were doing so at a time of decreased food availability. In addition, ringtailed lemurs have an epitheliochorial placenta which may be less efficient for nutrient transfer (Jolly, 1984). Pregnant ringtailed females should therefore be expected to exhibit specific feeding and foraging behaviors that may differ from nonreproducing individuals.

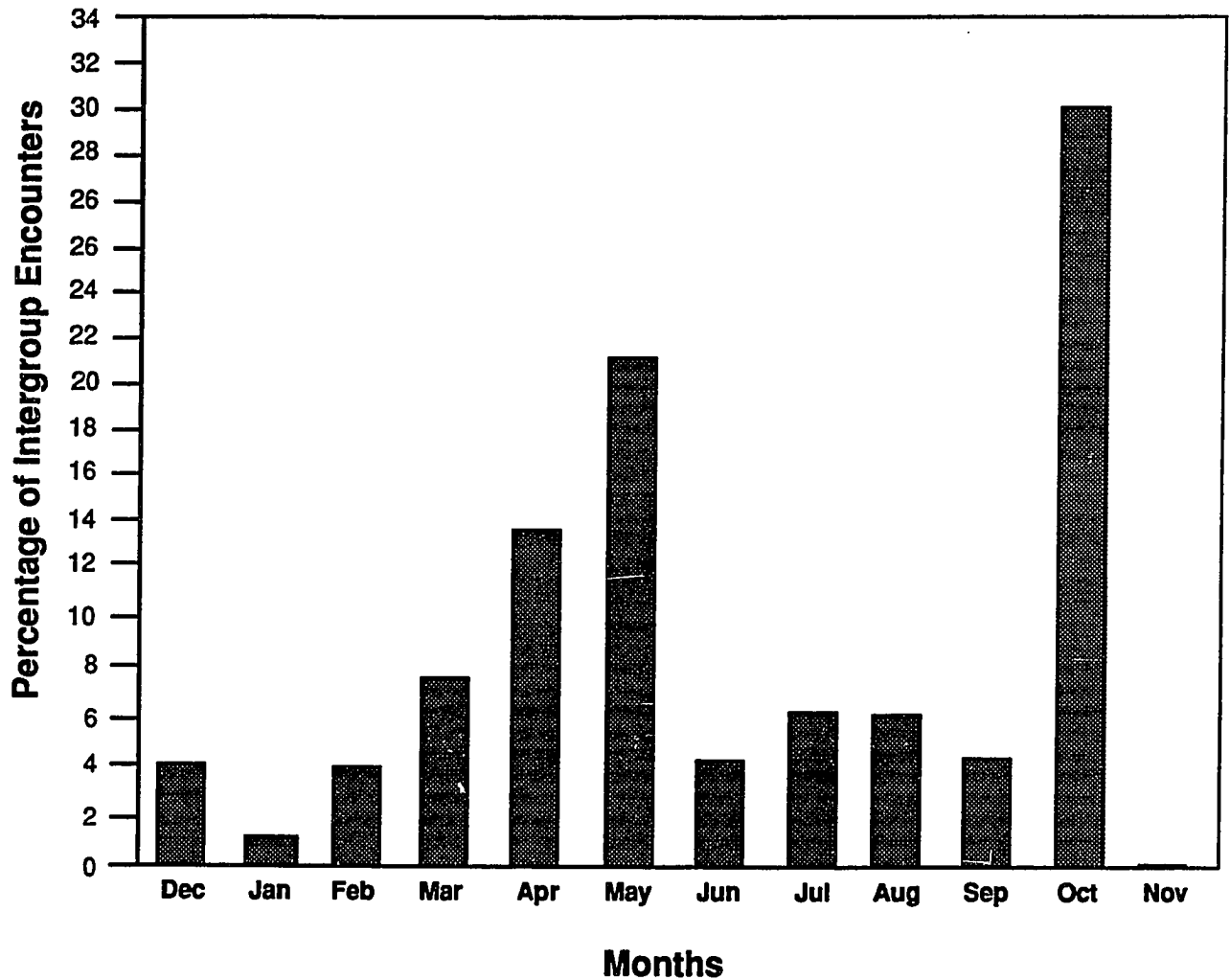


Figure 3.1. Percentage of Intergroup Encounters Between Green and Black Troop and Other Troops of Ringtailed Lemurs at Beza Mahafaly, 1987-1988.

MATERNAL INVESTMENT AND FEEDING ECOLOGY

While few studies on free-ranging mammals have focused on the effects of maternal investment on feeding ecology, their results indicate that a female's feeding behavior changes in quantifiable ways as she proceeds through pregnancy and lactation (Sheep: Hadjipieris and Holmes, 1966; Red Deer: Clutton-Brock et al, 1982a; Black-tailed Deer: Sadleir, 1982).

Primate females, in general, may be expected to exhibit variability in feeding ecology associated with reproduction due to their relatively high maternal investment (Dunbar and Dunbar, 1988). The limited information available from primate field studies suggests that lactating females may spend more time feeding than other individuals (Yellow baboon: Post, 1978; Howler monkey: Smith, 1977), may have equal or greater mean daily energy intake than larger males (Yellow baboon: Stacey, 1986; Olive baboon: Barton, 1989; Rhesus macaque: Marriott, et al, 1989), may increase time spent feeding as lactation proceeds (Cotton-top tamarins: Kirwood and Underwood, 1984; Galagos: Sauther and Nash, 1986; Yellow baboon: Altmann, 1980; Gelada baboon: Dunbar and Dunbar, 1988), may consume more protein rich food items such as pith, young leaves, shoots and invertebrates (Wedge-capped capuchins: Fragasy, 1986; *Cercopithecus* sp.: Gautier-Hion, 1980; Green monkeys: Harrison, 1983b), and may have a greater mean rate of intake for total dry weight and protein than cycling females (Yellow baboon: Barton, 1988). During pregnancy, females may focus on certain food types (Baboons: Silk 1987a).

There is recent evidence that Malagasy lemurs may be under especially high energetic stress during reproduction (Jolly, 1984; Young, et al., 1990). Jolly (1984) points out that strepsirrhine primates produce smaller neonates than haplorhine primates, which may be more costly to the mother during lactation because she must maintain the infant during a higher rate of postnatal growth. While many strepsirrhines potentially mitigate some of these demands by leaving infants in nests, *L. catta* females, who also produce small neonates, carry their infants with them (Jolly, 1984). More recently, Young et al. (1990) have demonstrated that the Malagasy lemurs also have a higher rate of prenatal investment than lorisiformes. This, tied with a relatively low basal metabolic rate, indicates that they may be under greater potential reproductive stress than other strepsirrhines, specifically the Lorisiformes. Female dominance in these species (such as *L. catta*) thus may be related to both high maternal investment and a seasonal food supply. The documentation of a seasonal food reduction in food availability in relation to reproductive events has not been directly tested in the field for any diurnal

Malagasy lemur. Data from this study are used to explore such a relationship.

ACTIVITY BUDGETS AND REPRODUCTION

One way to adapt to the increased costs associated with gestation and lactation is to alter activity patterns. It has been generally assumed that females deal with increasing costs associated with lactation by increasing time spent feeding as lactation proceeds, although this relationship has only been demonstrated for two baboon species in the field (Altmann, 1980, Dunbar and Dunbar, 1988). Because increased feeding time logically suggests less time available for other activities, it has been variously suggested that social time (Altmann, 1980) or time spent resting (Dunbar and Dunbar, 1988) are the marketable activity states that should vary accordingly. In Altmann's view, both resting and moving are viewed as constants. Therefore to increase feeding time as lactation proceeds, a female would curtail social interactions. Dunbar and Dunbar (1988) argue that social time for female primates should be conserved as methods for maintaining important coalitions. Based on data on free-ranging gelada baboons they suggested that it was resting time that was altered, social time was modified only when feeding demands were too high to be met by increased resting. Activity budgets were compared for classes of individuals to determine this relationship in ringtailed lemurs.

SEX DIFFERENCES IN FEEDING ECOLOGY

Sex differences in feeding ecology have been documented for a number of free-ranging primate species. This includes differences in feeding levels and feeding sites (*Colobus badius*: Clutton-Brock, 1973; *Indri indri*: Pollack, 1977; *Callicebus torquatus*: Kinzey, 1977; *Pongo pygmaeus*: Rodman, 1977; *Papio cynocephalus*: Post, 1981; *Pan troglodytes*: Wrangham, 1979; Galdikas and Teleki, 1981;), time spent feeding (*Colobus badius*: Clutton-Brock, 1974; *Indri indri*: Pollack, 1977; *Allouatta villosa*: Smith, 1977; *Cercocebus albigena*: Waser, 1977; *Symphalangus syndactylus*: Chivers, 1977; *Gorilla gorilla berengei*: Fossey and Harcourt, 1977, Watts, 1988), as well as food choice (*Pongo pygmaeus*: Rodman, 1977; *Cercocebus albigena*: Waser, 1977; *Indri*

indri: Pollack, 1977; *Papio cynocephalus*; Rhine, 1978; *Pan troglodytes*: McGrew, 1979; Galdikas and Teleki, 1981; Boesch and Boesch, 1981; *Theropithecus gelada*: Iwamoto, 1979; *Callicebus moloch*: Wright, 1984; *Cebus olivaceus*: Robinson, 1986; *Cercopithecus nictitans*, *C. cephus*, *C. pogonias*: Gautier-Hion, 1980; *Cercopithecus sabaeus*: Harrison, 1983b). Two common explanations for such sex differences in feeding behavior have been sexual dimorphism and the cost of reproduction (Clutton-Brock, 1977b). Because it is difficult to separate the effects of body size from that of reproductive state, dimorphism in body size has confounded attempts to interpret sex differences in feeding behavior for dimorphic primates. Adult *L. catta*, and other Malagasy primates, have minimal body size dimorphism (see Harvey, et al., 1987), thus the role of reproductive condition in creating sex differences in feeding behavior can be clarified.

RESULTS

LACTATION

Activity Levels and Reproductive Condition

One way females could reduce the cost of lactation would be to reduce their activity levels. Table 3.1 compares time spent resting for lactating and nonlactating females and for males. In both troops lactating females spent more time resting than nonlactating females and males. However, males and nonlactating females did not differ markedly in time spent resting. When time spent nursing was subtracted, the differences between lactating females, males and nonlactating females were not significant, indicating that increased time resting was directly associated with lactation. Table 3.2 compares mean time spent allogrooming by the different classes of individuals. The two classes of females did not differ markedly in time spent allogrooming. Males spent markedly less time allogrooming than nonlactating females. Mean total time spent feeding did not differ between lactating and nonlactating females or males (lactating females = 26%; nonlactating females = 25%; males = 22%).

Table 3.1. Comparisons of mean time spent resting during the wet season for males, for lactating and non-lactating females.

GREEN TROOP	Wet Season
Males	22%
Lactating females	30%
Non-lactating females	25%
Lactating females vs Non-lactating females	$p < .05$
Males vs Lactating females	$p < .05$
Males vs Non-lactating females	n.s.

BLACK TROOP	Wet Season
Males	36%
Lactating females	45%
Non-lactating females	32%
Lactating females vs Non-lactating females	$p < .02$
Males vs Lactating females	$p < .05$
Males vs Non-lactating females	n.s.

* Note that each percentage is relative to that class only (e.g. time spent resting by males is a percentage of total activity by males only). Thus these percentages will not tally to 100%.

Table 3.2. Comparison of the mean time spent allogrooming by males and by lactating and non-lactating females during the wet season.

WET	*ALLOGROOM
Lactating	2.00
Non-lactating	2.75
Males	1.48
Lactating vs. Non-lactating	n.s
Lactating vs. Males	n.s.
Non-lactating vs. Males	p <.03

* As percentage of total activity.

To look at activity states in a manner comparable to Dunbar and Dunbar (1988), median values were determined for total time spent feeding, time spent resting, and time spent feeding on leaves and fruits for lactating and nonlactating females (Fig. 3.2-3.5). Median time spent feeding was similar for males, lactating and nonlactating females. Resting was greater in lactating females, but all classes showed the same pattern. Although variable, from month to month, nonlactating females had higher levels of allogrooming than other classes. There was an inverse relationship for allogrooming between lactating and nonlactating females (Fig. 3.2). Generally, when nonlactating females increased allogrooming, lactating females decreased this social activity. Males spent similar time allogrooming as lactating females in months 1-2 but for the rest of the period they maintained a low level of social grooming. Fig 3.2 also compares time spent feeding with resting. There was an inverse relationship between resting and feeding for all classes of individuals, i.e. as resting increased, time spent feeding decreased and vice versa. The relationship between median time spent feeding, resting and allogrooming is illustrated in Fig 3.3-3.4. In general, there was an inverse relationship between feeding and allogrooming for lactating and nonlactating females, but not for males. All classes of individuals dramatically decreased

time spent allogrooming in month 3 whereas they increased feeding at the same time. Resting also decreased during month 3 for males and lactating females which corresponds with increased feeding time. Lactating females showed an inverse relationship between resting and allogrooming specifically during months 1-2 and months 4-6. For nonlactating females and, to a lesser extent, for males resting tended to match time spent allogrooming. There was a decrease in feeding, resting and allogrooming during month 4 for nonlactating females.

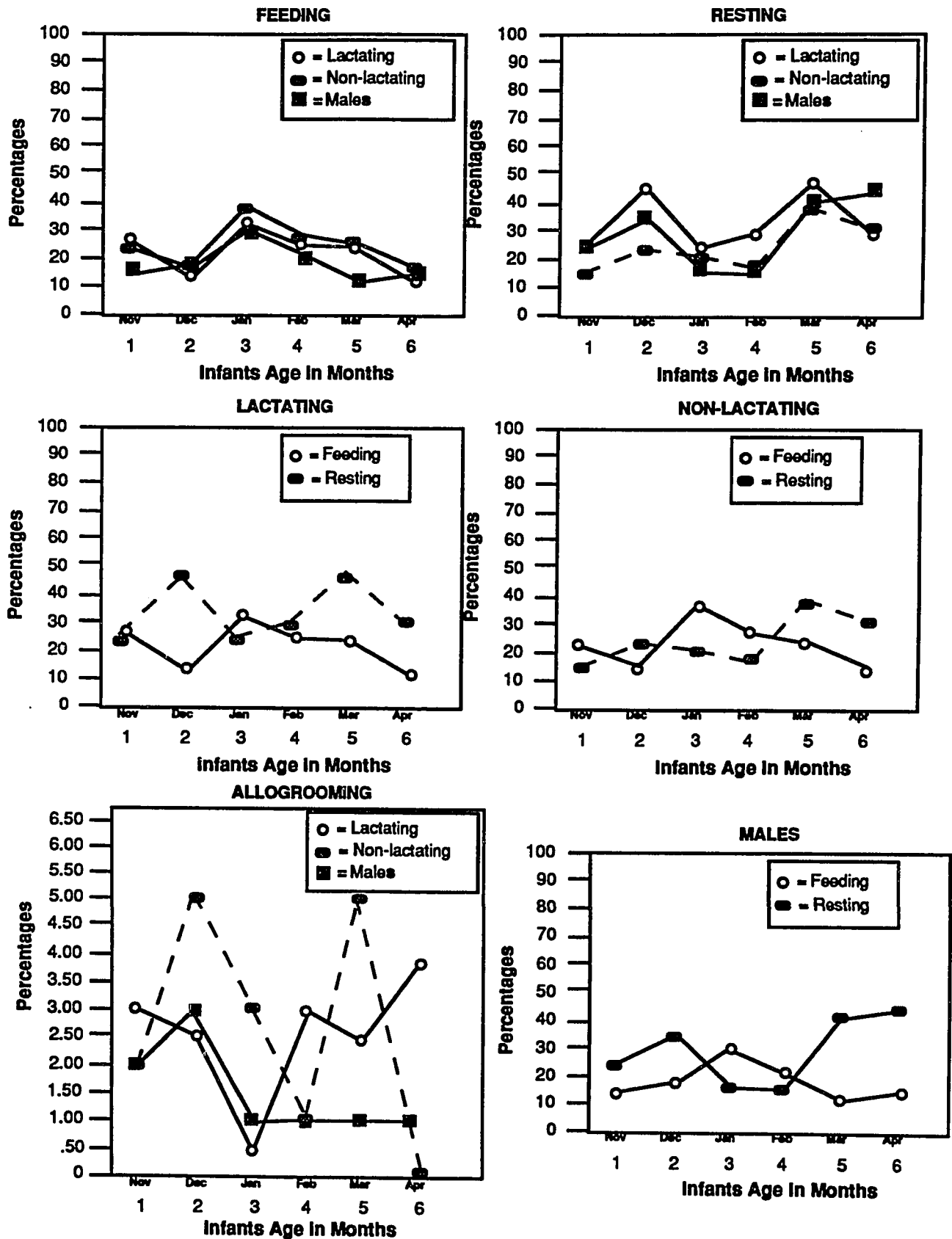


Figure 3.2. Median Percentages of Time Spent Feeding, Resting, and Allogrooming.

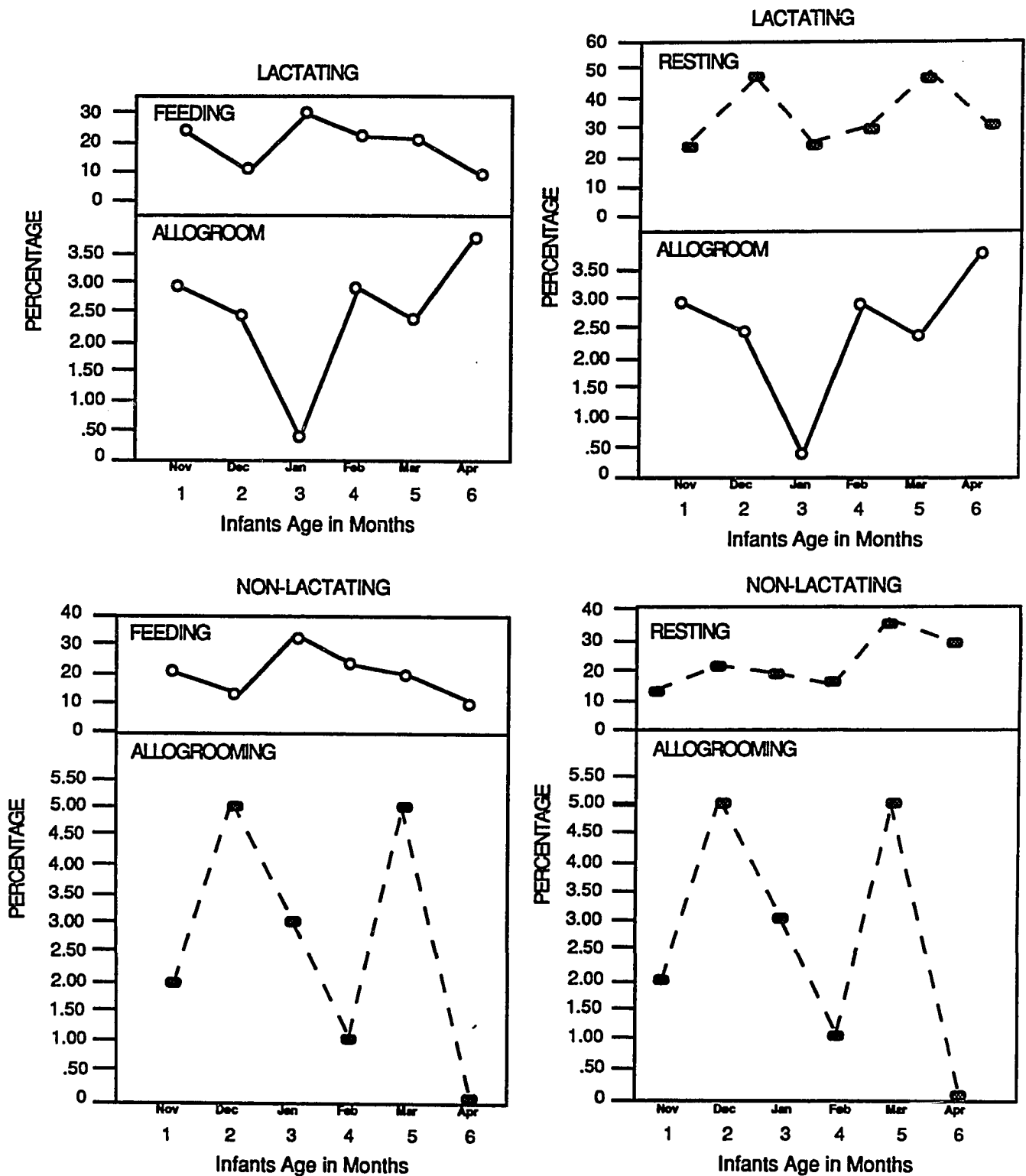


Figure. 3.3 Comparison of Median Time Spent Feeding, Resting and Allogrooming in Lactating and Non-lactating Females

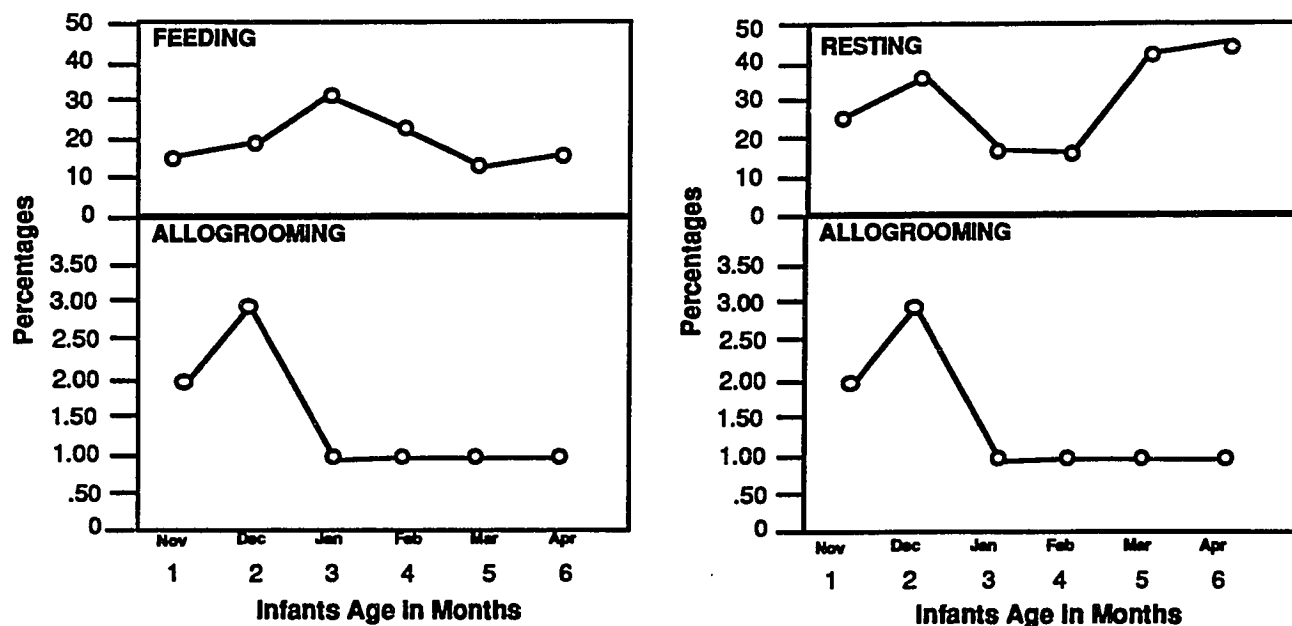


FIG. 3.4. Comparison of Median Time Spent Feeding, Resting and Allogrooming by Males During the Wet (Lactation) Season.

Fig 3.5 illustrates median time spent feeding on leaves and fruits and compares this to phenological data. Lactating females spent more time feeding on leaves, but the general pattern of leaf feeding is the same for all classes. This pattern does not agree well with the availability of leaves during this period. In fact the pattern is generally inverse, with higher median rates of leaf feeding when availability was low, and vice versa. For fruits, nonlactating females showed higher levels, but again the general pattern is the same for all individuals. This pattern closely matches the availability of fruits during the same period.

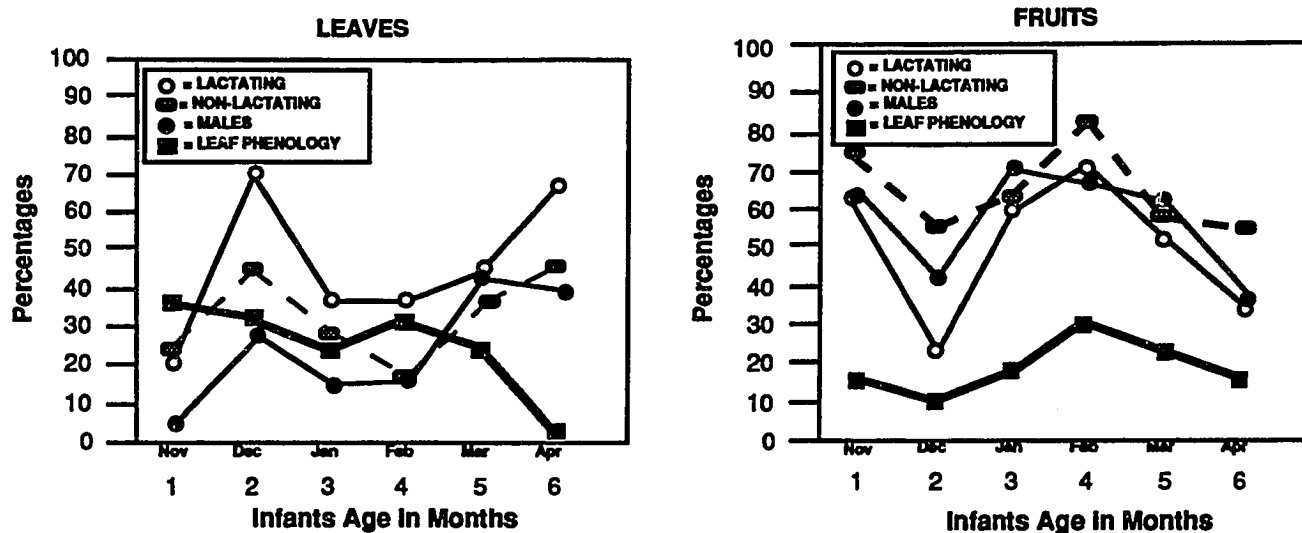


Fig. 3.5 Median Percentages of Time Spent Feeding on Leaves and Fruits by Males, Lactating and Non-lactating Females, with a Comparison with Fruit Phenology.

Feeding Behavior

The feeding behavior of lactating females was different from nonlactating females and males. Time spent feeding gradually increased during the first few days of lactation. This pattern continued for at least three weeks thereafter (Fig. 3.6). Use of food types varied by class. Lactating females ingested greater amounts of young leaves (mainly herbaceous terrestrial species) than either males or nonlactating females (Fig. 3.7). Males also ingested greater weights of young leaves than nonlactating females. In the category of fruit *Tamarindus indica* pods (TIFR) were separated from other fruit. This was done because TIFR is qualitatively different from other fruits (see Chapter 4: Top 20 Foods by Type). Lactating females fed less on fruits (not including TIFR) than both males and non-lactating females, and they fed less on TIFR than did non-lactating females (Fig. 3.8). There were no significant differences between males and nonlactating females for fruits excluding TIFR. However, low ranking males did feed more on TIFR than any other class. High ranking males and lactating females fed on similar, low amounts of TIFR.

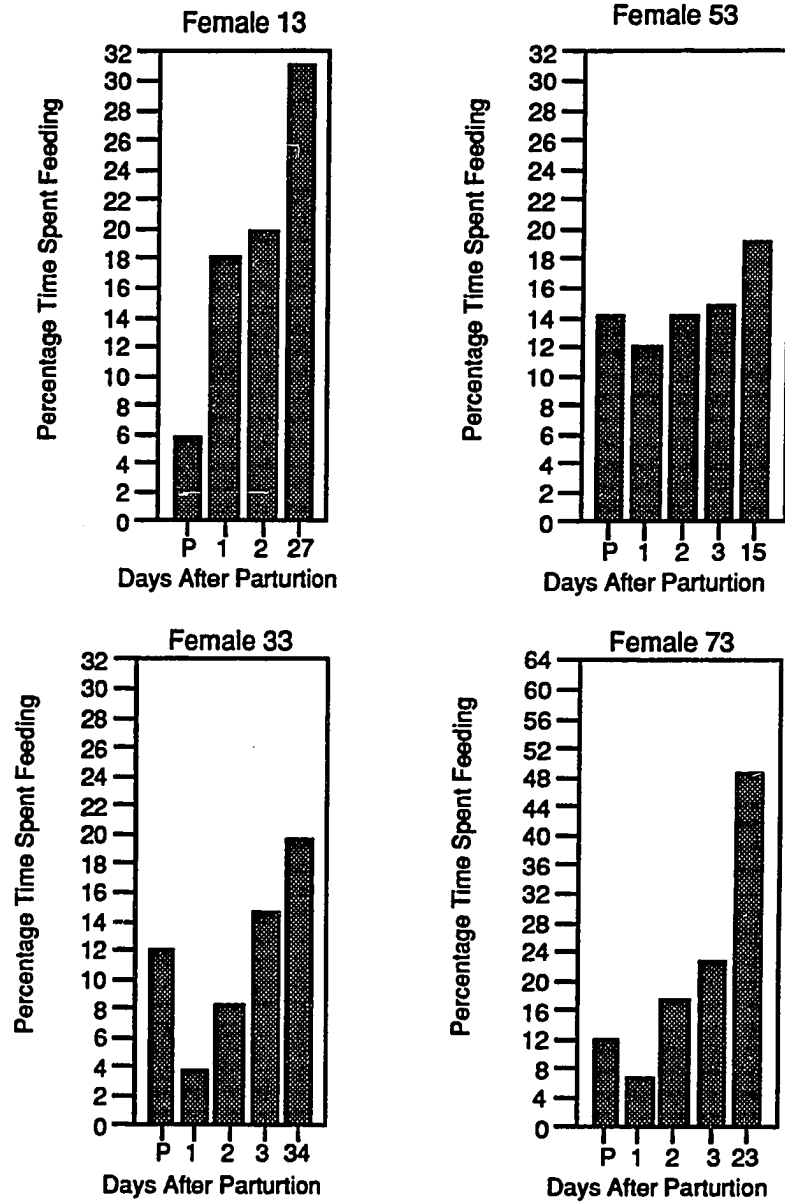


Figure. 3.6 Percentage of Time Spent Feeding During Early Lactation by *Lemur catta* females.

Young Leaves

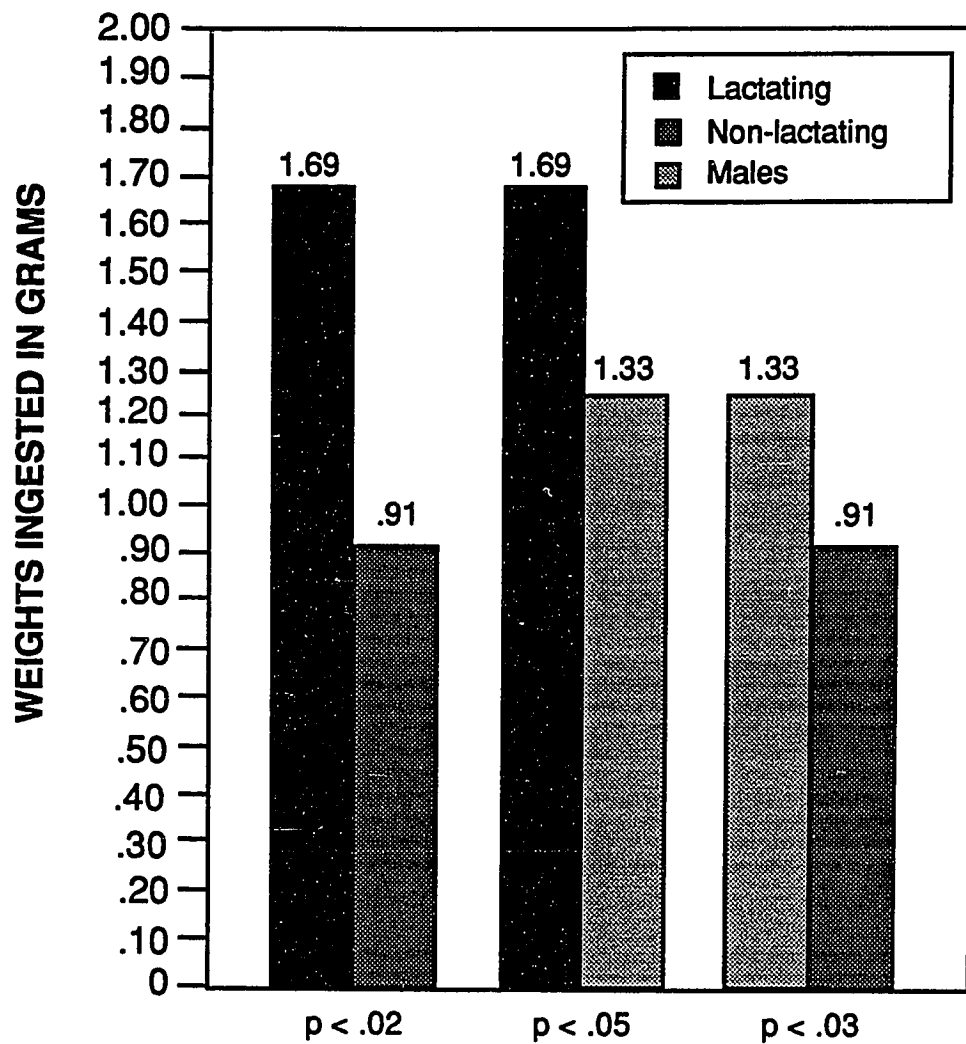


Figure. 3.7. Mean Minimum Amount Ingested by Weight of Young Leaves by Lactating and Non-lactating Females and by Males.

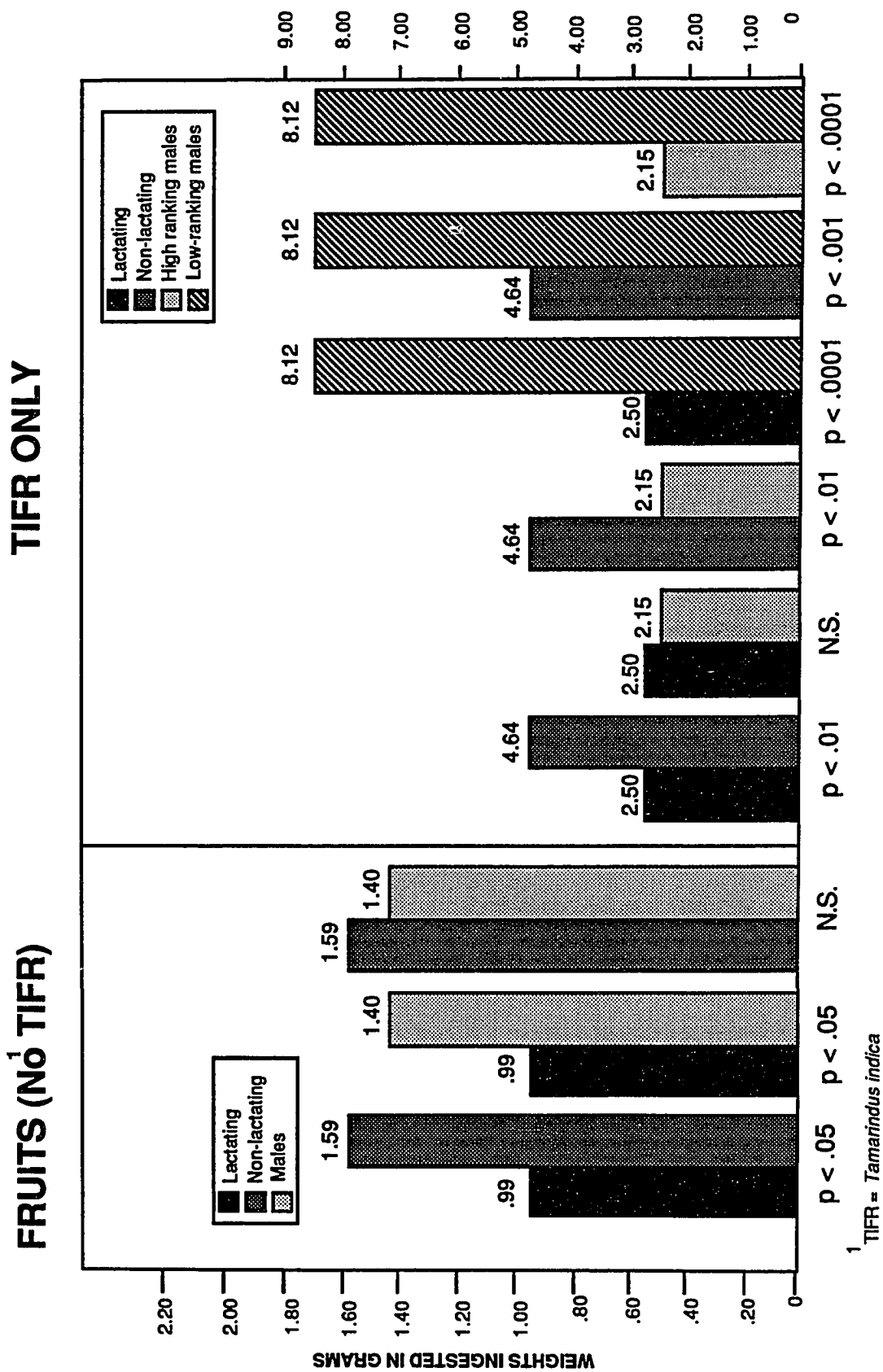


Figure. 3.8. Mean Minimum Weights Ingested of Fruits by Males, Lactating and Non-lactating Females During the Wet Season.

Table 3.3 compares the use of fruit and leaf species. In general, lactating females used the same mean number of species of fruits as did nonlactating females, but they tended to use more species of leaves. Males and lactating females did not differ significantly in numbers of fruit or leaf species used. Males did utilize more species of leaves than nonlactating females. While nonlactating females used approximately the same number of fruit and leaf species, both males and lactating females used more leaf species than fruit species.

Table 3.3. Comparison of the mean number of fruit and leaf species used by males and by lactating and non-lactating females during the wet season.

WET	Fruit Species	Leaf Species	Fruit vs. Leaf Species
Lactating	2.45	3.95	$p < .004$
Non-lactating	2.78	2.96	n.s.
Males	2.17	3.54	$p < .002$
Lactating vs. Non-lactating	n.s.	$p < .05$	
Lactating vs. Males	n.s.	n.s.	
Non-lactating vs. Males	$p < .03$	$p < .05$	

Ringtailed lemurs rarely foraged for leaves, but they did forage for fruits. No consistent differences relative to reproductive state could be found for fruit foraging (wet season: lactating females = 9%; nonlactating females = 10%; males = 8%). To determine the relationship between time spent feeding and time spent foraging on fruits a feeding efficiency ratio was used (total time spent feeding + total time spent foraging). When the ratio is 1 an individual spends equal time feeding and foraging. Ratios greater than 1 indicate more time spent feeding (more efficient), whereas ratios less than 1 denote that the individuals spend more time foraging (less efficient). Comparing males, lactating and nonlactating females indicates that lactating and nonlactating females were equally efficient feeding on fruits (Fig. 3.9). Males, however, showed more efficient ratios of fruit feeding than either lactating or nonlactating females. To determine why this was the case, efficiency ratios for particular fruits were compared (Table 3.4). From this table it is evident that males are more efficient at feeding on *T. indica* fruits than either class of females. There are no marked differences in feeding efficiency for the other main fruits fed on during the wet season.

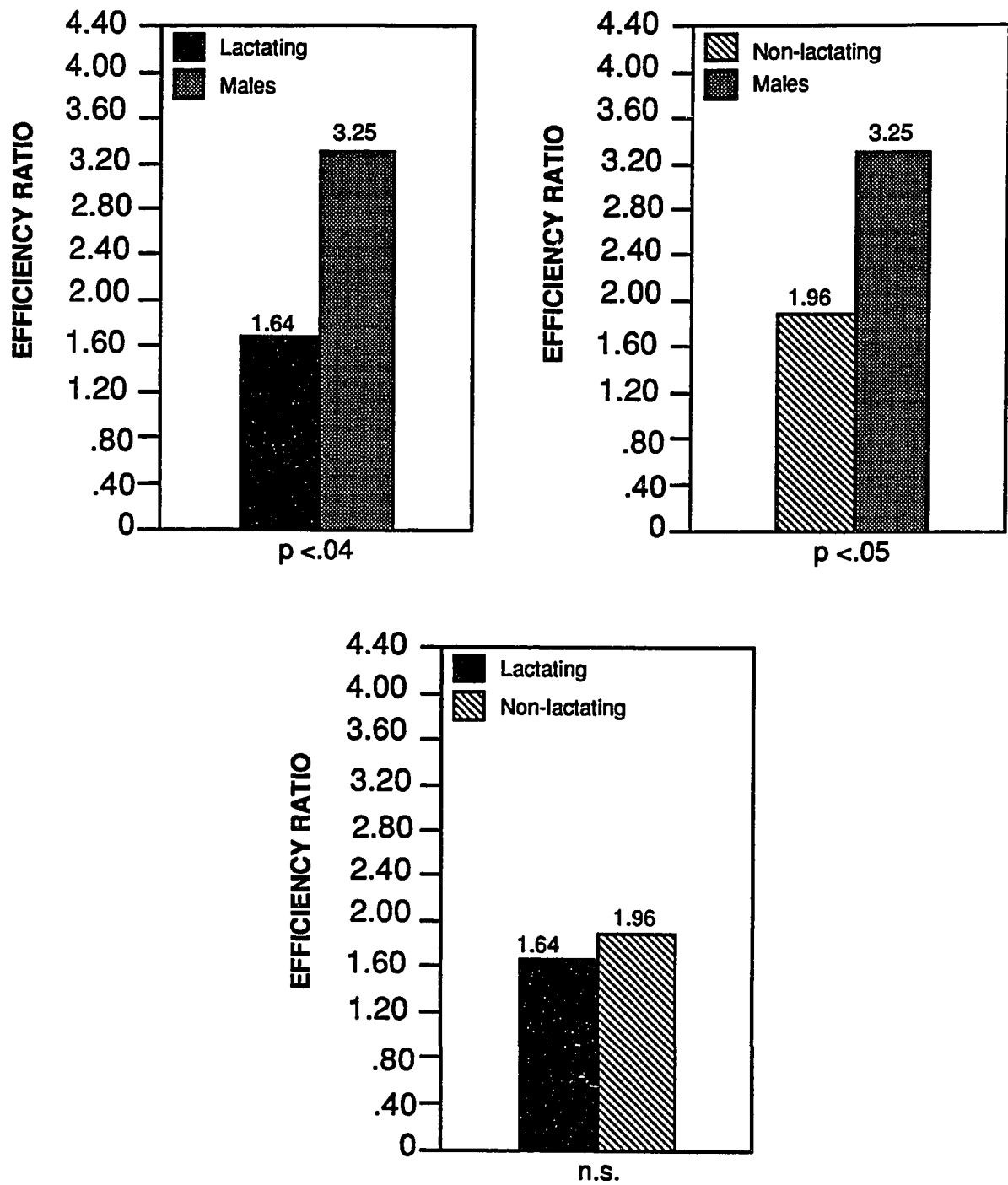


Figure. 3.9. Comparison of Feeding Efficiency on Fruits During the Wet Season Between Males, Lactating and Non-lactating Females.

Table 3.4. Efficiency ratio for feeding on main fruits during the wet season by lactating and non-lactating females and by males.

	<i>Tamarindus indica</i>	<i>Talinella dolphinensis</i>	<i>Grewia sp.</i>
Lactating	1.50	1.50	.73
Non-lactating	1.52	1.92	.66
Males	2.71	1.82	.73
Lactating vs. Non-lactating	n.s.	n.s.	n.s.
Lactating vs. Males	$p < .05$	n.s.	n.s.
Non-lactating vs. Males	$p < .05$	n.s.	n.s.

When looking at specific fruit species, the trend of lactating females feeding less on fruits is supported for some but not all plant species. This can be seen in Table 3.5. Feeding on *Talinella dolphinensis* during the wet season was significantly less for lactating females, even less than the males. Lactating females also fed less on the fruits of *T. indica* during the wet season. However, for *Grewia clavata* fruits this is not seen, and clearly other factors are also important, and will be discussed in Chapter 4.

Table 3.5 Comparisons of the mean minimum weights ingested of selected fruits during the wet season by males and by lactating females.

	<i>Talinella dolphinensis</i>	<i>Tamarindus indica</i>	<i>Grewia clavata</i>
Lactating	.20*	.99	.41
Non-lactating	.43	1.58	.52
Males	.65	1.39	.48
Lactating vs. Non-lactating	p <.02	p <.05	n.s.
Lactating vs. Males	p <.02	p <.05	n.s.
Non-lactating vs. Males	n.s.	n.s.	n.s.

There is a large population of termites within the forest, with termites building large nests inside of dead trees, as well as terrestrial mounds. Although soil from termite mounds or trails of termites was commonly eaten or licked by all individuals, there were also sex differences. During the wet season males spent more time licking and eating termite soil than either class of females (Fig. 3.10). Lactating females, on the other hand, used this item less than both males and nonlactating females.

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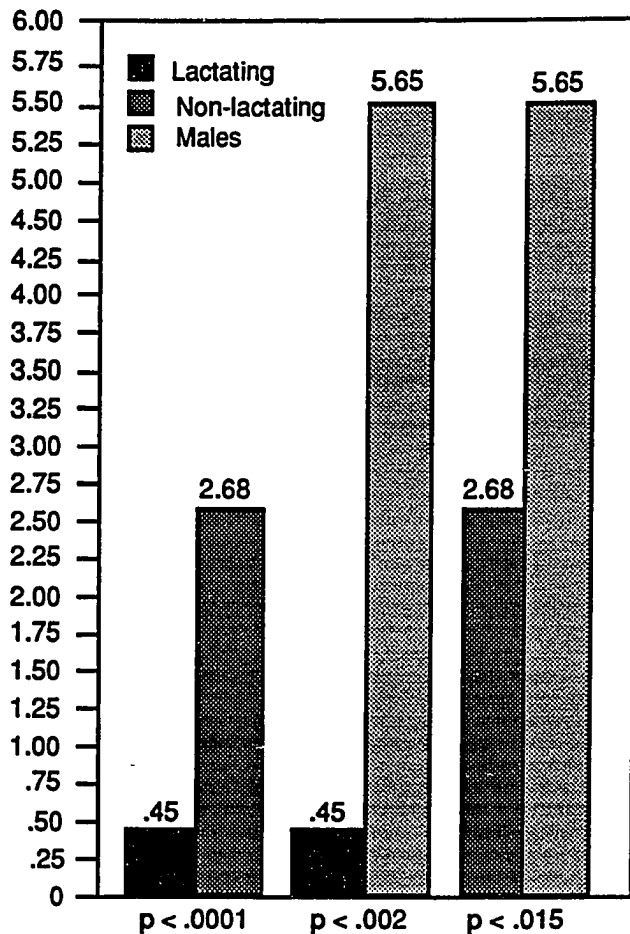


Figure. 3.10. Time Spent Feeding and Licking Termite Soil by Males and Lactating and Non-lactating Females During the Wet Season.

Use of the Environment

Table 3.6 compares use of different forest levels by the three classes of individuals. Lactating females used the environment differently than did nonlactating females. While nonlactating females fed more in the trees, nursing females fed more at ground level, where they focused on young leaves. Lactating females also spent twice as much time feeding in bushes. Males behaved similarly to lactating females. They spent more time feeding at ground level and in bushes than nonlactating females, and they fed less in the trees than nonlactating females. These different classes are compared with respect to time spent feeding on fruits and/or leaves at different levels in

Table 3.7. At ground level, males spent more time feeding on fruits (specifically the fruits of *Tamarindis indica*, which ripen and fall to the ground in large quantities). Both males and lactating females fed more on leaves at ground level (especially herbaceous plants). There were no meaningful differences between the different classes for time spent feeding on fruits in bushes, but lactating females fed more on leaves in bushes than either nonlactating females or males. Nonlactating females fed more on fruits in trees than either lactating females or males. Lactating females fed more on leaves in the trees than did males and nonlactating females, although this was significant only with respect to the males.

Table 3.6. Comparisons of the mean percentage of time spent feeding at different levels by lactating and non-lactating females and by males.

	Ground Level	Bush	Tree
Lactating	29%	11%	60%
Non-lactating	18%	4%	78%
Males	30%	13%	57%
Lactating vs. Non-lactating	p<.01	p<.001	p<.05
Lactating vs. Males	n.s.	n.s.	n.s.
Non-lactating vs. Males	p<.02	p<.002	p<.05

Table 3.7. Comparisons of the mean percentage of time spent feeding on fruits and leaves at different levels by lactating and non-lactating females and by males.

FRUITS	Ground	Bush	Tree
Lactating	9%	3%	44%
Non-lactating	9%	6%	60%
Males	14%	7%	48%
Lactating vs. Non-lactating	n.s.	n.s.	p<.04
Lactating vs. Males	p < .05	n.s.	n.s.
Non-lactating vs. Males	p < .05	n.s.	p<.05

LEAVES	Ground	Bush	Tree
Lactating	16%	10%	18%
Non-lactating	10%	3%	12%
Males	18%	5%	8%
Lactating vs. Non-lactating	p <.05	p <.01	n.s.
Lactating vs. Males	n.s.	p <.04	p <.002
Non-lactating vs. Males	p <.01	n.s.	n.s.

Lactating females might also reduce energy expended by using less expensive modes of movement. Table 3.8 compares time spent moving on the ground and in the trees. Total time spent moving in the trees and on the ground did not differ between lactating and nonlactating females, but males did spend more time moving on the ground and less time moving in the trees than either lactating or nonlactating females. Modes of movement might also vary and this is shown in Table 3.9. Movement was partitioned as more active (climb, run, leap, hop, jump) and less active (walk). Active movement in the trees did not vary markedly between reproductive states, but movement on the ground involved more active forms for nonlactating females when compared to lactating females. Males spent less time utilizing active forms of movement in the trees, but were more active on the ground when compared to lactating females. Males and nonlactating females did not vary markedly on these measures. Walking at ground level did not vary between the reproductive states, but lactating females spent less time walking at tree level than did nonlactating females. Males spent more time walking at ground level than nonlactating females, but did not differ from lactating or nonlactating females in time spent walking at tree level.

Table 3.8. Comparisons of the mean percentage of movement at different levels by males and by lactating and non-lactating females.

	Ground	Tree
Lactating	43%	57%
Non-lactating	42%	58%
Males	54%	46%
Lactating vs. Non-lactating	n.s.	n.s.
Lactating vs. Males	p <.01	p <.01
Non-lactating vs. males	p <.01	p <.01

Table 3.9. Comparisons of the mean percentage of active movement and walking at different levels by males and by lactating and non-lactating females.

	ACTIVE		WALK	
	Ground	Tree	Ground	Tree
Lactating	3%	41%	37%	19%
Non-lactating	9%	35%	29%	27%
Males	9%	30%	39%	22%
Lactating vs. Non-lactating	p <.01	n.s.	n.s.	p < .05
Lactating vs. Males	p<.003	p<.015	n.s.	n.s.
Non-Lactating vs. Males	n.s.	n.s.	p < .01	n.s.

THE MATING SEASON

Activity Budgets

Ringtailed lemurs have a very seasonal mating pattern, and at Beza Mahafaly all observed matings occurred in May (Sauther, 1991). During the mating season three females (female 82 of Black Troop, 73 and 53 of Green Troop) and one male (male 10 of Green Troop) were followed continuously during the days prior to, during, and just after mating. Actual mating was observed for all individuals except female 73, who apparently mated after dusk as she was followed daily and no mating was observed. This female did exhibit a copulatory "plug" (made of hardened ejaculate) and subsequently gave birth. Captive studies indicate that the copulatory plug forms within minutes in the vaginal canal of ringtailed lemurs, but is visible between 1-2 days after mating (Evans and Goy, 1968). Mating is estimated for this female based on first observance of the plug, and behavioral changes by troop males who cease to sexually approach females after females have gone through behavioral estrus, have mated, and are no longer sexually receptive (Sauther, 1991). Percentages of time spent resting and feeding by each individual are presented in Fig. 3.11. All individuals spent less time feeding and more time resting throughout this period. The day of mating was characterized by a peak in resting, and a decrease in time spent feeding. Resting was also higher at this time than during the sample period 1-2 weeks before (10: 40% versus 28%; 53: 40% versus 35%; 82: 48% versus 39% ; 73: 45% versus 38%). Feeding was lower relative to the earlier sample (10: 9% versus 12%; 53: 11% versus 15%; 82: 7% versus 11%; 73: 10% versus 15%). There is a negative correspondence between resting and feeding for most days, i.e. as resting increases, feeding decreases. Time spent autogrooming and allogrooming is presented in Fig. 3.12. Allogrooming is low for all individuals throughout this period, but autogrooming either remains high (female 82, 73, male 10) or increases on the days prior to mating (female 53). Relative to the sample 1-2 weeks before, allogrooming was lower (10: 3% versus 5%; 53: 1% versus 2%; 82 1% versus 3%; 73: .05% versus 1%) and autogrooming was higher (10: 9% versus 6%; 53: 4% versus 1%; 82: 4% versus 3%; 73: 4% versus 1%).

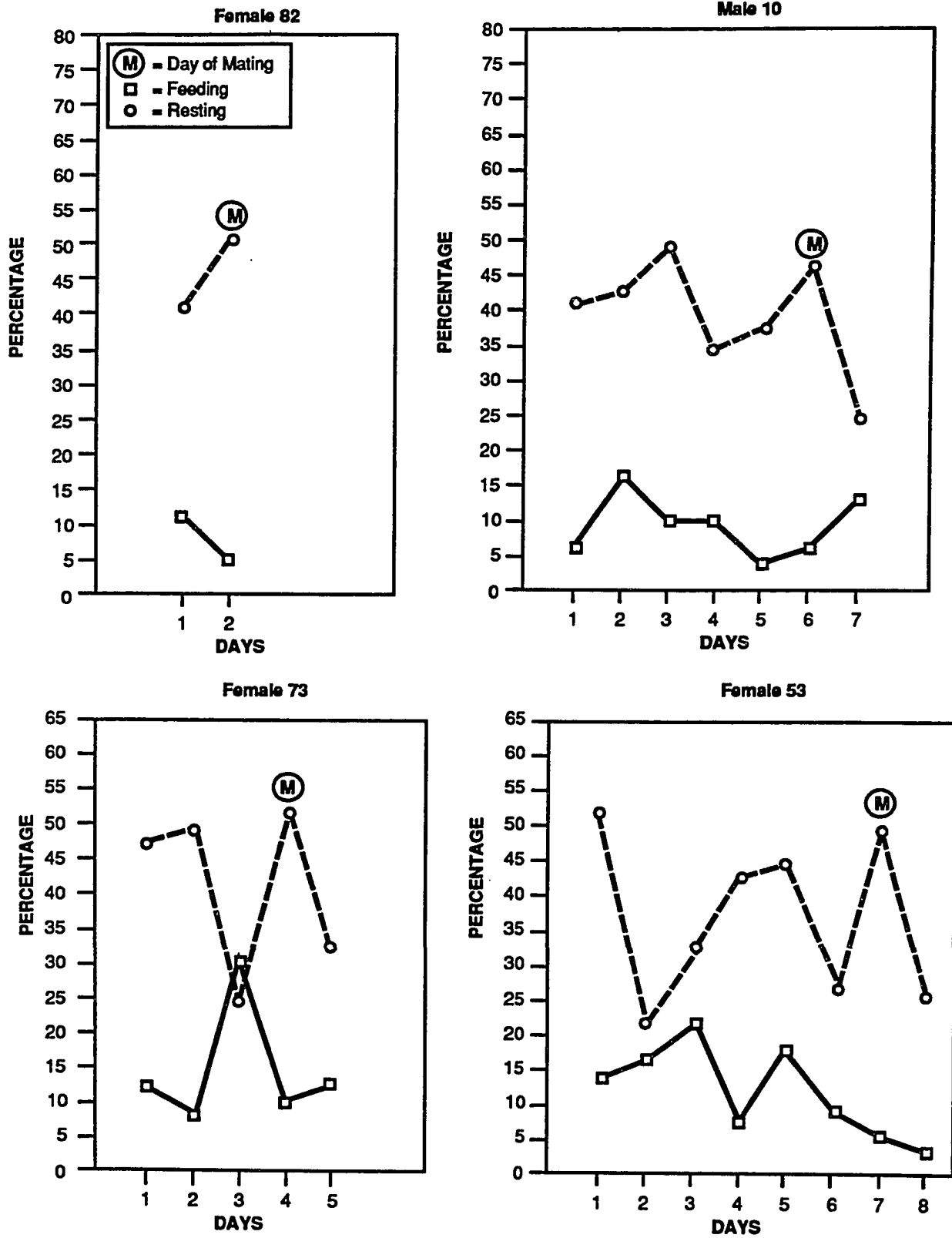


Figure. 3.11 Percentage Time Spent Feeding and Resting During Mating Season Day Follows.

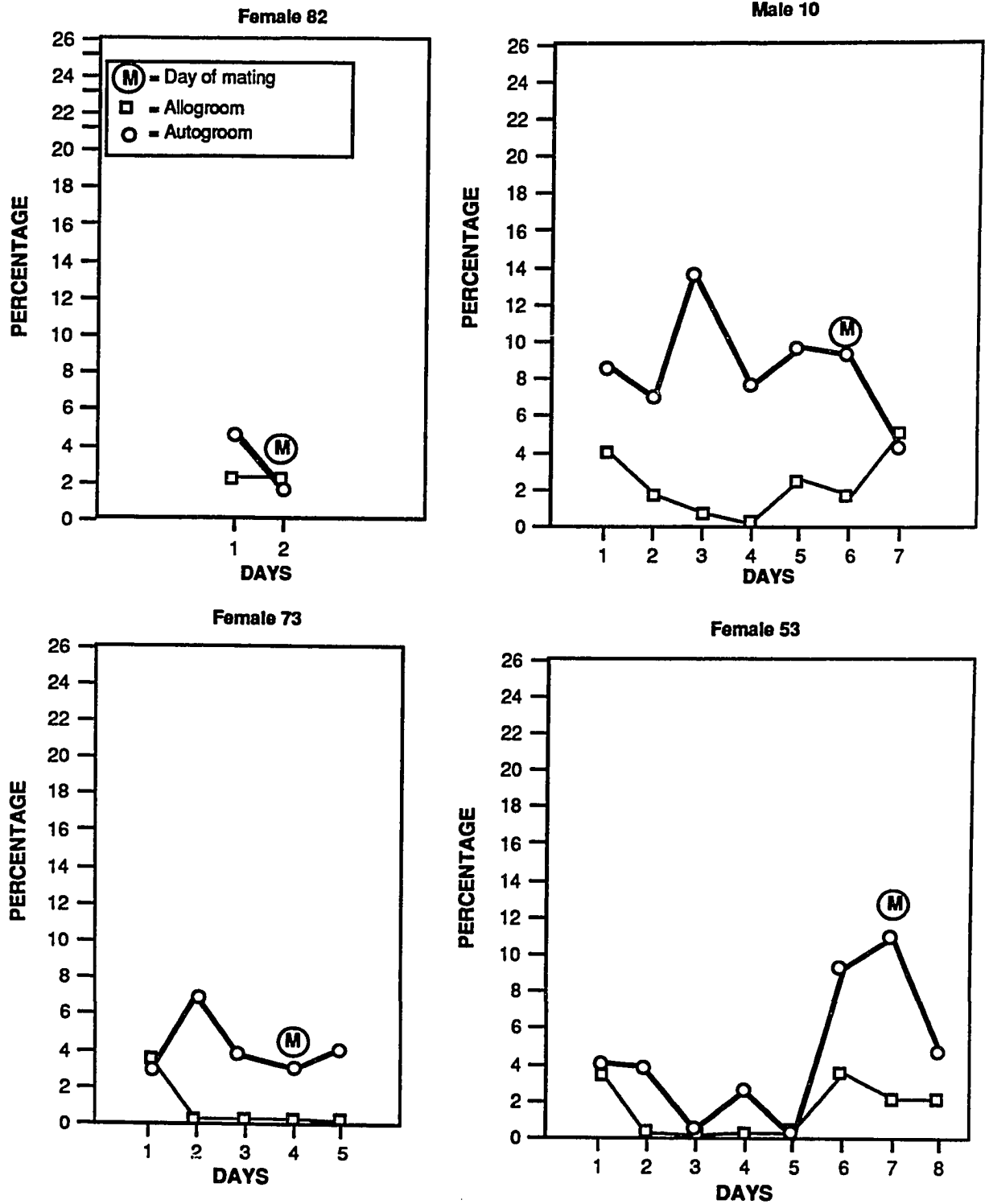


Figure. 3.12 Percentage Time Spent Allogrooming and Autogrooming During Mating Season Day Follows.

Major Food Parts Utilized

Fig. 3.13 diagrams the percentage of time spent feeding on major food parts during this period. There is a sex difference in that prior to mating the male focused on mature leaves, whereas the females spent a higher percentage of their time feeding on fruits. For females 82, 53 and male 10, the day of mating was characterized by a peak in time spent feeding on the fruits of *T. indica* and *Enterospermum pruinosa*, (*T. indica* : 10 = 60%, 73 = 69%, 53 = 43%, 82 = 44%; *E. pruinosa* : 10 = 20%, 73 = 6%, 53 = 54%, 82 = 44%), and a considerable decrease in time spent feeding on young leaves. Female 73, who mated at night or early morning, showed just the opposite pattern as she fed more on leaves and less on fruit.

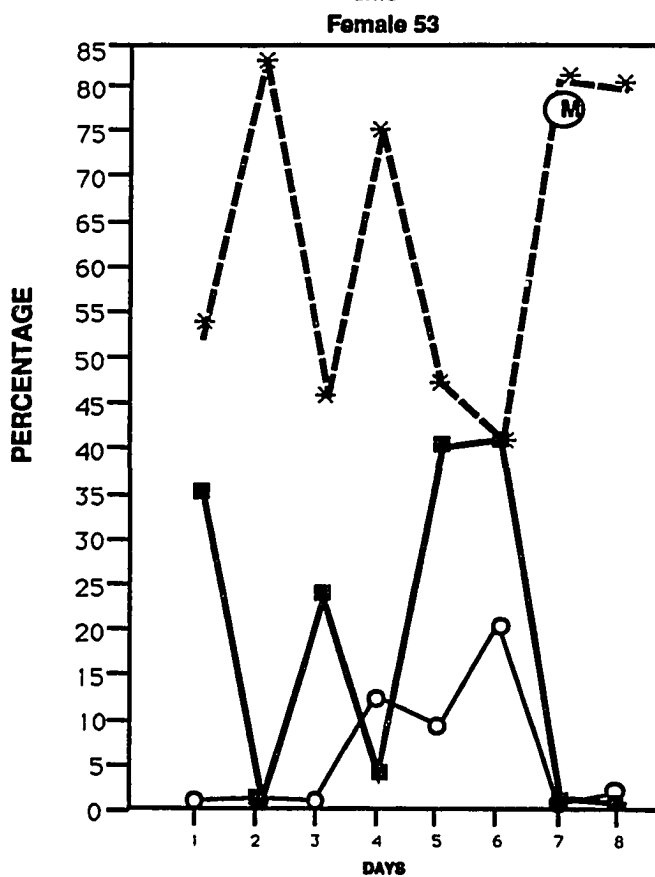
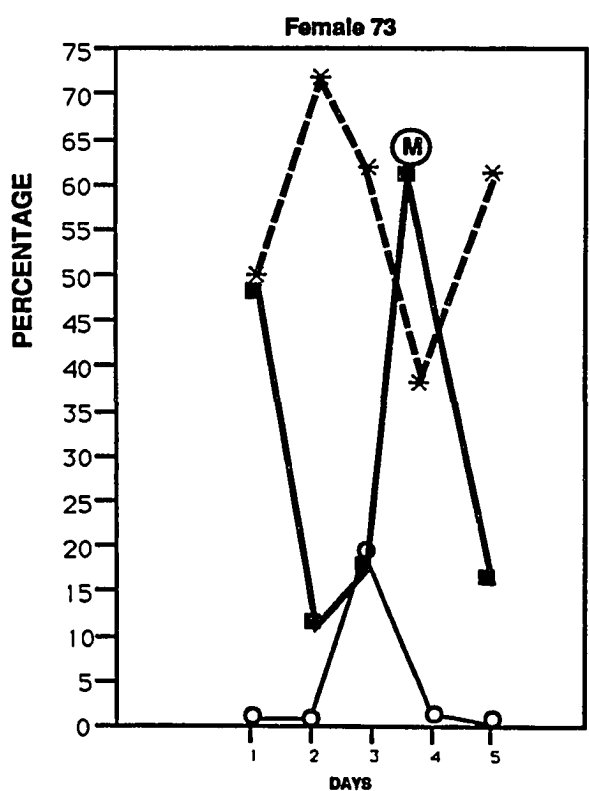
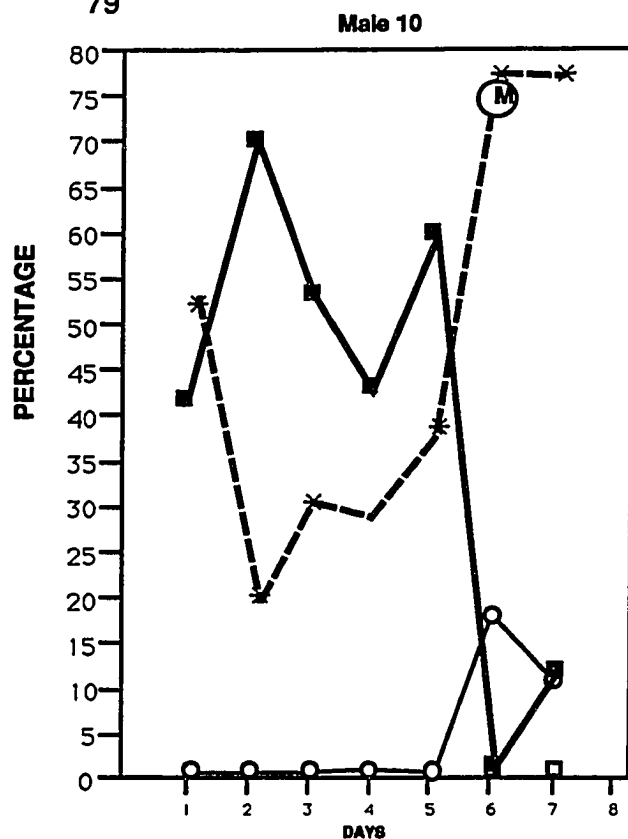
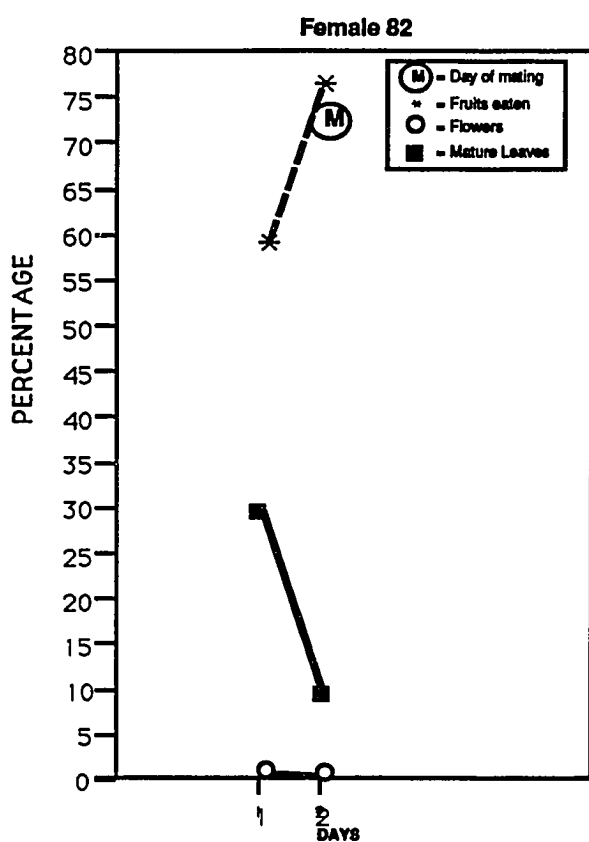


Figure. 3.13 Percentage Time Spent Feeding on Major Food Parts During Mating Season Day Follows.

Feeding Behavior of Consorting Pair

During daily observations of female 53, male 10, who was the central male of her troop (Sauther, 1991), followed her closely. For example, he was this female's nearest neighbor in 53% of the observations, far exceeding any other male or female individual. His behavior was recorded simultaneously, and a comparison of time spent resting and feeding by the pair is presented in Fig. 3.14. The activity patterns of these two individuals were strikingly similar during this time. Time spent feeding on major food parts by female 53 and male 10 are shown in Fig. 3.15. There is little correspondence between the two for time spent feeding on flowers of *T. indica*, but for fruits, and young leaves the patterns of daily use is similar. This is especially striking for time spent feeding on fruit on the day of mating, as well as the day before and after mating.

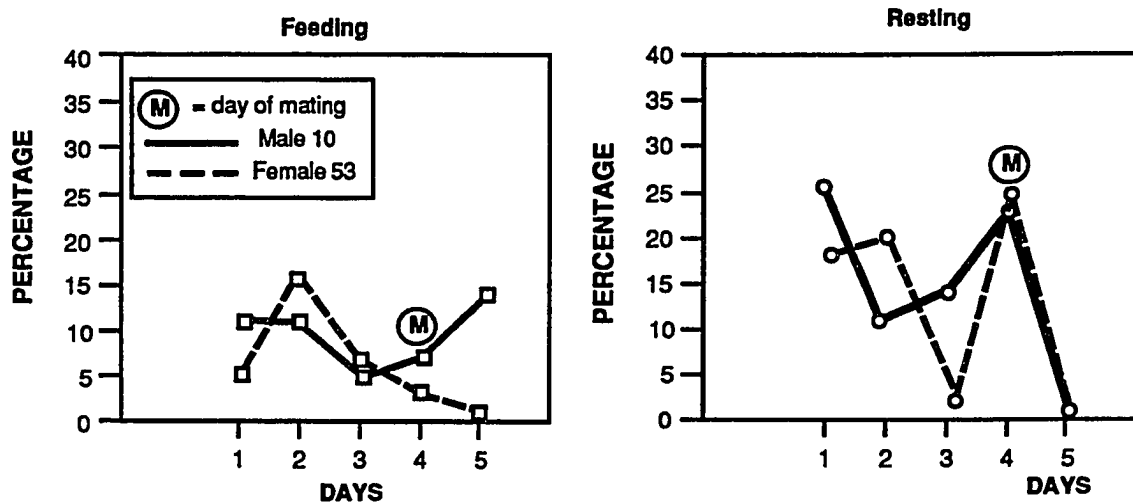


Figure 3.14 Percentage Time Spent Feeding and Resting by Female 53 and Male 10 During Mating Season Day Follows.

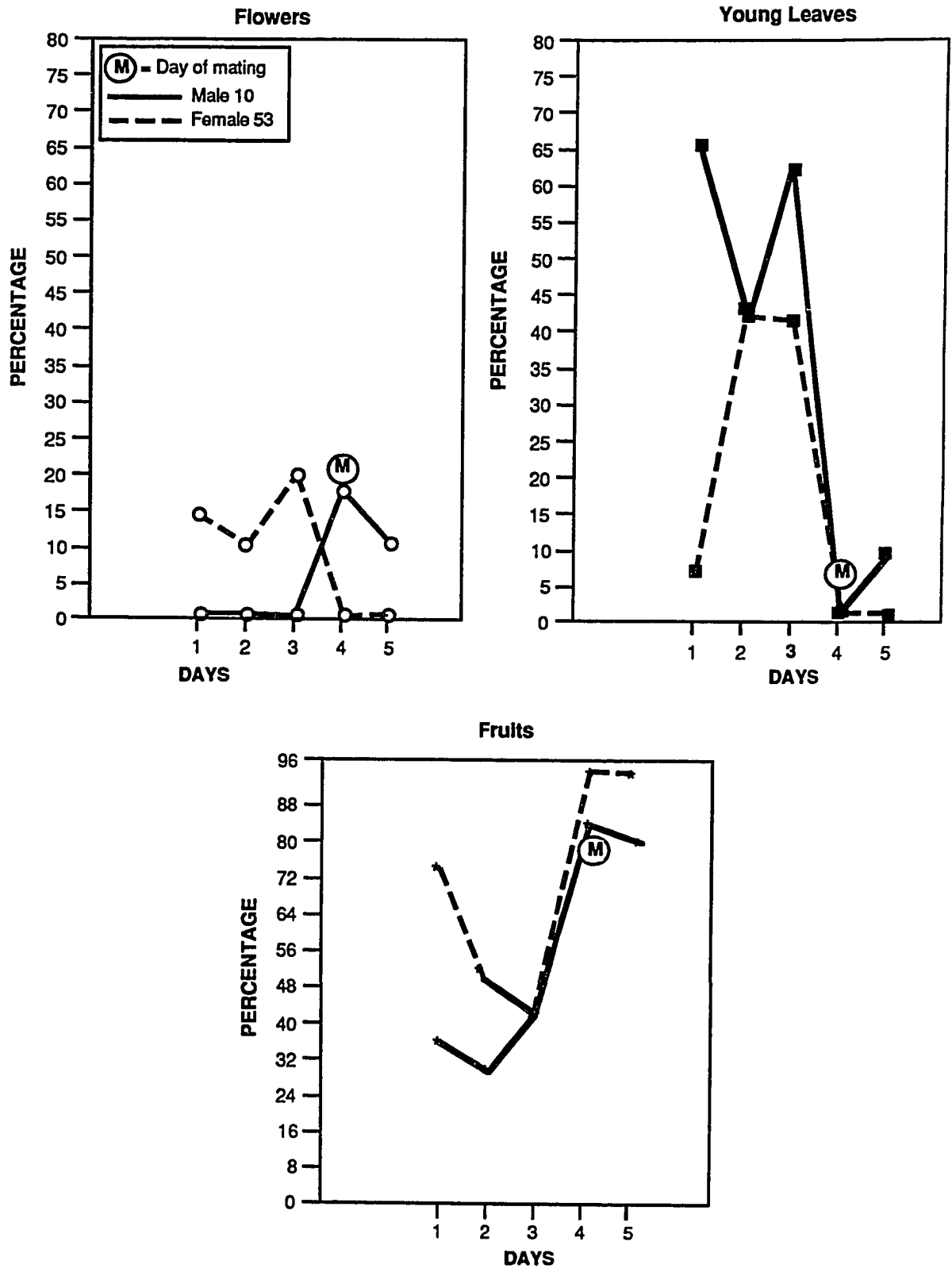


Figure. 3.15 Percentage Time Spent Feeding on Major Food Parts by Male 10 and Female 53 During Mating Season Day Follows.

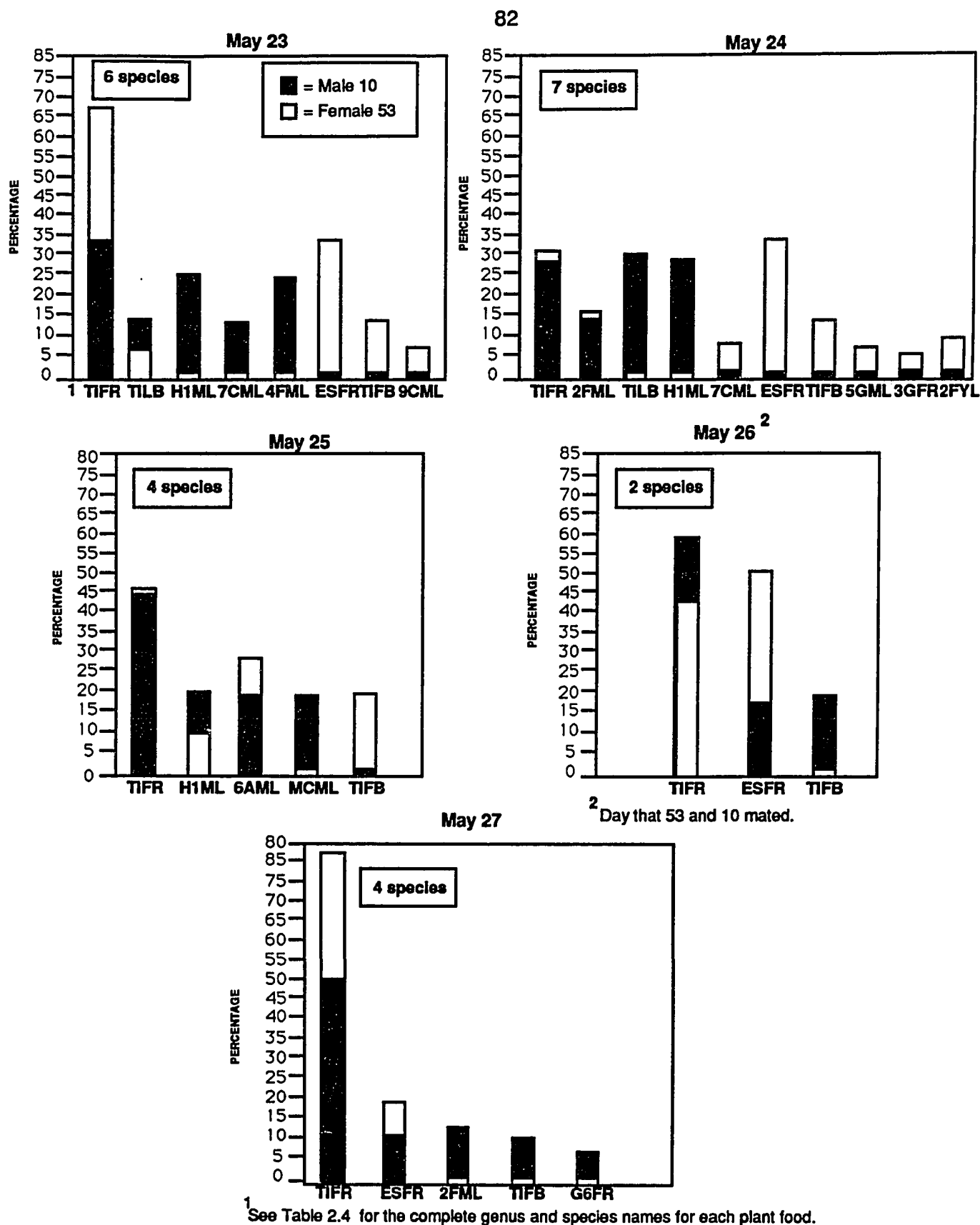


Figure. 3.16 Comparison of Species and Parts Eaten by Male 10 and Female 53 During Mating Season Day Follows.

In order to determine whether such correspondence reflects similar species used, time spent feeding on all species and parts are presented for each day the pair were followed in Fig. 3.16. For all days the closest correspondence between 53 and 10 is time spent feeding on the fruit of *T. indica* (TIFR in the figure). On the two days prior to mating, for example, their percentages are virtually the same. There is less correlation for the species of leaves consumed, although overlap does occur for some species such as *Commicarpus commersonii* (2FML in Fig. 3.16), *Secamone* sp. (H1ML), and *Metaporana parvifolia* (6AML) on the days just prior to mating. Thus, although the pattern of time spent feeding on leaves was similar between 53 and 10 (Fig. 3.16) the actual species of leaves used by the two shows more variation than the fruit species. Total number of species used by the pair is substantially reduced the day before mating (four species) and on the day of mating only two species were used.

Pregnancy

Because all females were pregnant, it is not possible to directly determine what effect pregnancy has on female *L. catta* feeding ecology. Males and pregnant females could be compared with season held constant, as there is little body size dimorphism in this species. Thus, differences observed are not readily attributable to body size differences.

Activity Levels and Reproductive Condition

In Green Troop all individuals, male and female, spent more time resting during the dry season when compared to the wet season. In Black Troop this was true only for the males. For both troops the males and also the females who had lactated during the wet season rested more than did the females who had not lactated (Table 3.10).

Table 3.10. Time spent resting during the dry season by males, pregnant females who had lactated, and by pregnant females who did not lactate during the wet season.

GREEN TROOP	Dry Season	Wet vs Dry	
Males	40%	22% vs 40%	p < .001
Females who lactated	40%	30% vs 40%	p < .01
Females who did not lactate	32%	25% vs 32%	p < .05
Females who lactated vs. females who did not lactate	p < .02		
Males vs females who lactated	n.s.		
Males vs. Females who did not lactate	p < .02		

BLACK TROOP	Dry Season	Wet vs Dry	
Males	44%	36% vs 44%	p < .05
Females who lactated	49%	45% vs 49%	n.s.
Females who did not lactate	31%	32% vs 31%	n.s.
Females who lactated vs. females who did not lactate	p < .02		
Males vs females who lactated	n.s.		
Males vs. Females who did not lactate	p < .02		

Males spent considerably less time allogrooming than pregnant females (Table 3.11). Mean reduction in time spent allogrooming is illustrated in Table 3.12. Females who had lactated did not significantly reduce time spent allogrooming, but both males and females who had lactated showed marked reduction when wet and dry seasons are compared.

Table 3.11. Comparison of the mean time spent allogrooming by males and by pregnant females during the dry season.

DRY	*ALLOGROOM
Pregnant Females Males	1.69 .97
Pregnant Females vs Males	$p < .02$

* As percentage of total activity.

Table 3.12. Comparison of the mean time spent allogrooming by males and by lactating and non-lactating females during the wet versus the dry season.

WET VS DRY	Allogrooming	
Females who Lactated	2.00 vs 1.85	n.s.
Females who did not lactate	2.75 vs 1.68	$p < .05$
Males	1.48 vs .97	$p < .04$

Median time spent feeding, resting, allogrooming and feeding on leaves and flowers relative to phenology are presented in Fig. 3.17 and 3.18. Both classes are highly synchronous in their activity patterns for resting and feeding. Generally speaking, feeding and resting showed a close correspondence for May - August, as feeding time decreased so did resting time and vice versa. However, from August-September there is an inverse relationship between feeding and resting. Specifically, during September

feeding increased while both allogrooming and resting decreased for males and pregnant females. This correlates with an increase in the availability of both leaves and especially flowers during September (Fig. 2.4).

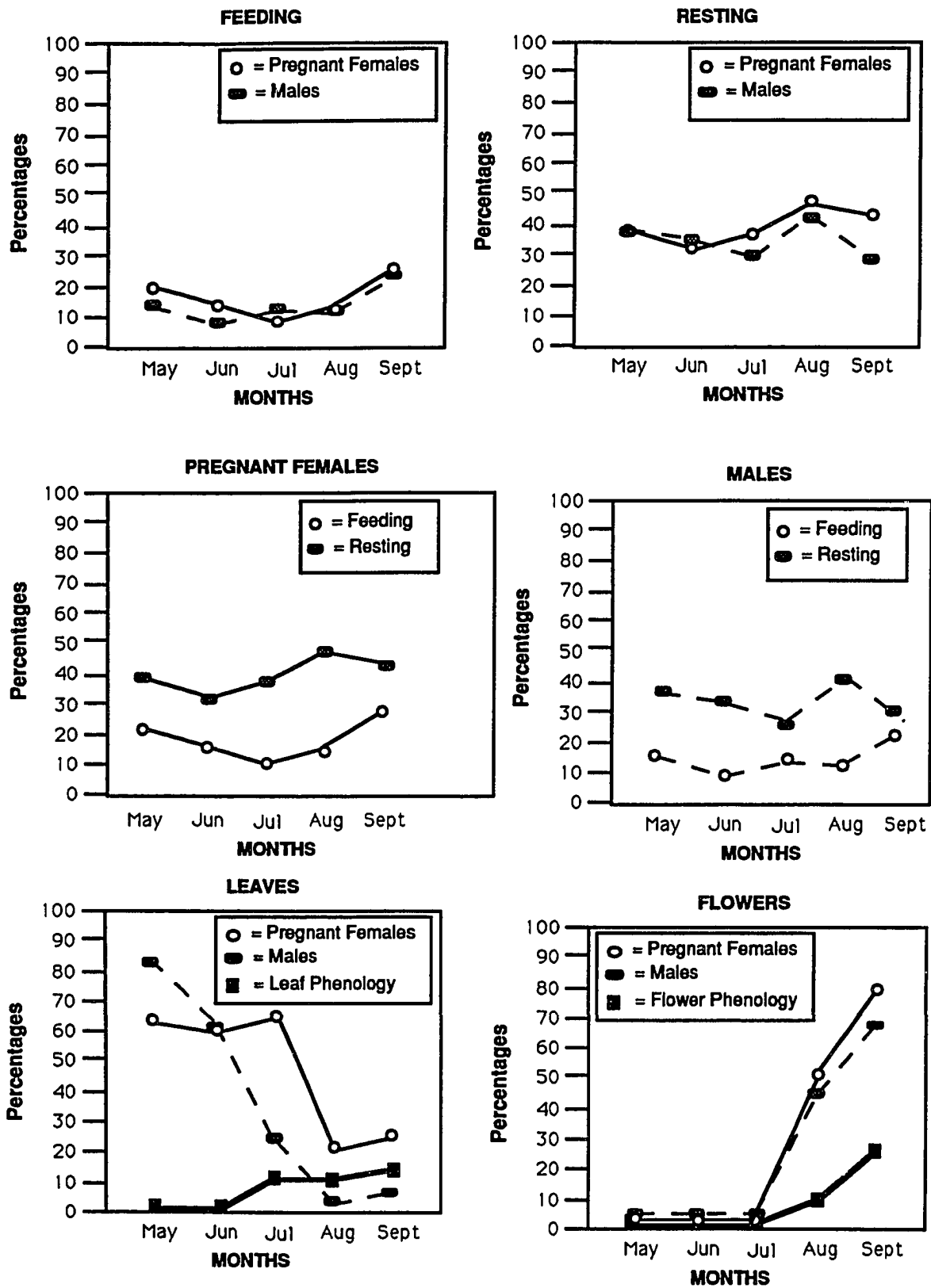


Figure 3.17 Median Percentages of Time Spent Feeding, Resting, and both for Males and Pregnant Females.

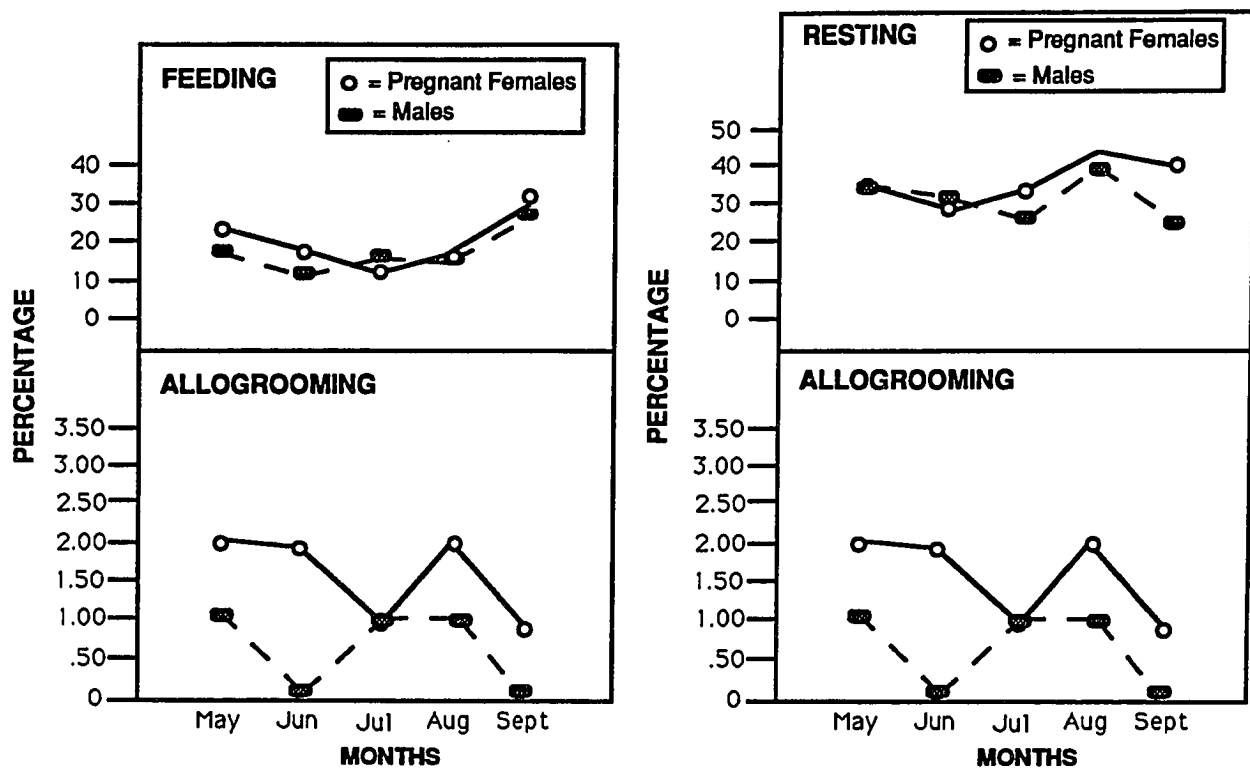


Figure. 3.18 Median Percentages of Time Spent Feeding, Resting, and Allogrooming by Pregnant Females and by Males.

Males and females both spent time feeding on flowers in proportion to their phenological availability. As in the wet season, both males and females showed considerable variability in time spent feeding on leaves relative to leaf phenology, which may reflect the dispersed nature of leaf distribution.

Effect of Previous Reproductive State

Because all females were pregnant during the dry season, it was possible to investigate how a female's previous reproductive state (lactating or nonlactating) affected her subsequent feeding behavior during pregnancy. Comparisons were made between time spent feeding on fruits and leaves (young leaves and leaf buds) during the wet season (lactation period) and the dry season (pregnancy). Females who lactated maintained high levels of leaf feeding during pregnancy (Fig. 3.19). Both pregnant females who had not lactated and males markedly increased feeding time on leaves. However, females who had not lactated had a greater increase in leaf use than did males, indicating this was related to pregnancy and not just reduced fruit availability (Fig. 3.20).

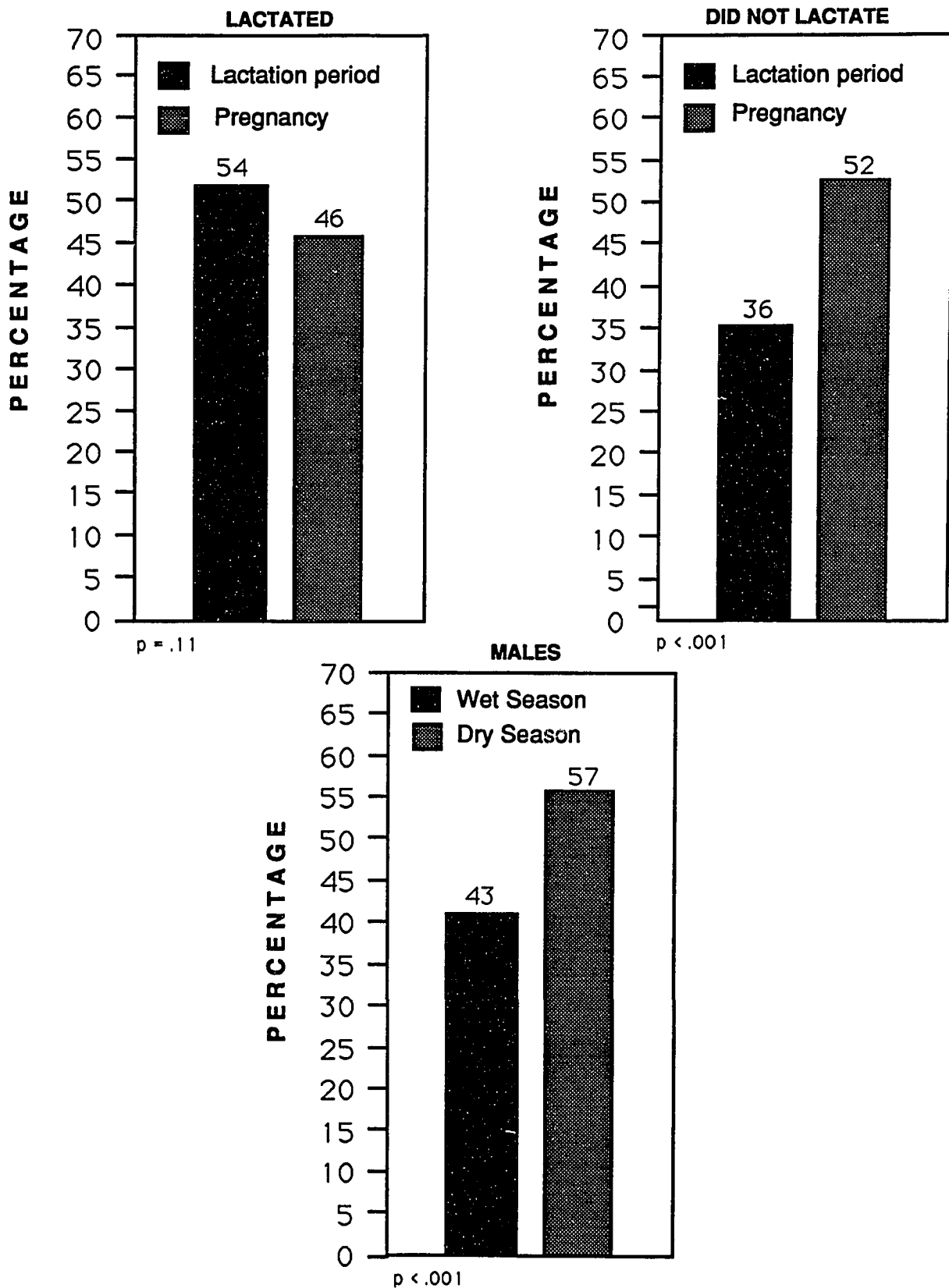


Fig. 3.19. Comparison of Percentage of Time Spent Feeding on Leaves During the Wet Season (Lactation Period) and the Dry Season (Pregnancy).

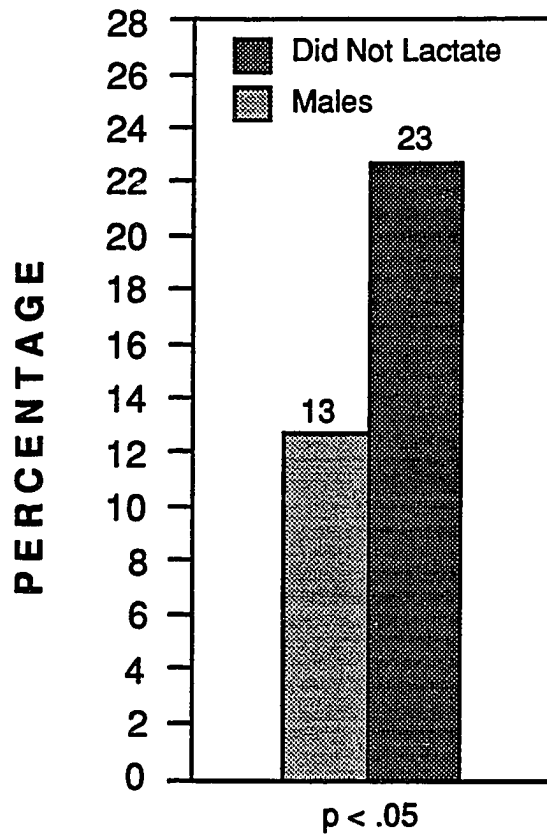


Fig. 3.20. Increase in Time Spent Feeding on Leaves from the Wet to the Dry Season For Males and for Females Who Did Not Lactate.

Fruits were less available during the dry season, and all individuals markedly decreased their use of fruits during this time. Females who had lactated during the wet season showed little reduction in time spent feeding on fruits when they were pregnant, (only 15% reduction) much less than either males (33% reduction) or females (44%) who had not lactated (Fig 3.21). Females who had not lactated had a greater reduction in time spent feeding on fruits when they were pregnant than did males. Females who had lactated spent more time feeding on fruits than either males or females who had not lactated (Fig. 3.22).

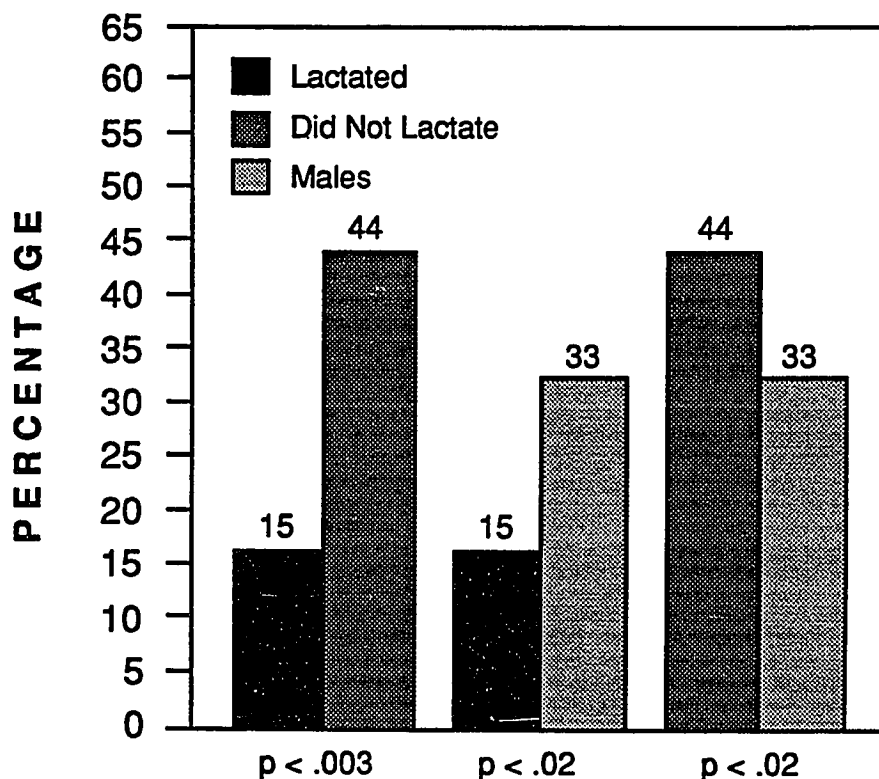


Figure. 3.21. Mean reduction In Percentage Time Spent Feeding on Fruits from the Wet to the Dry Season

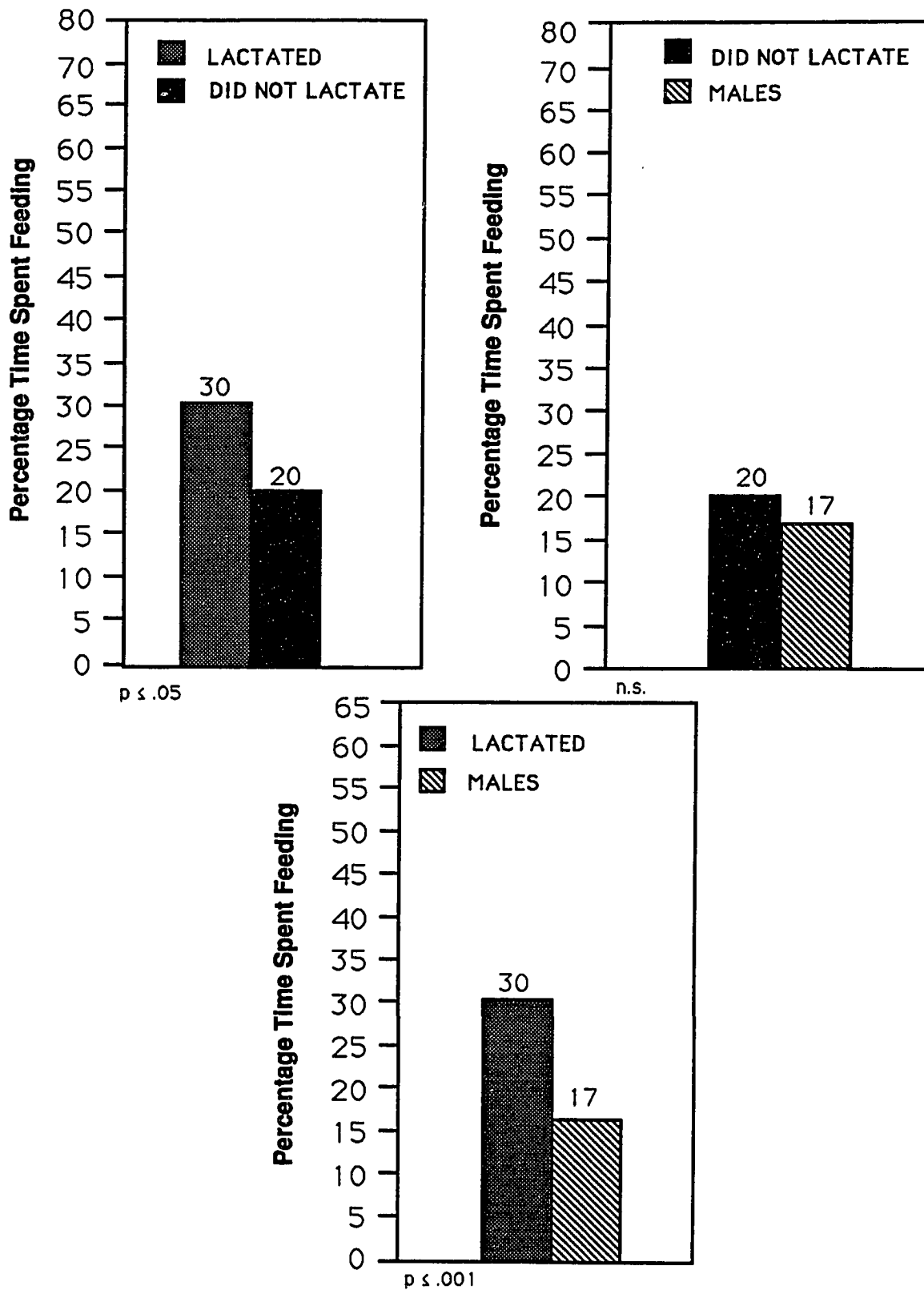


Fig. 3.22 Comparison of Time Spent Feeding on Fruit During the Dry Season by Females who had Lactated and Females who had not Lactated, and by Males.

Feeding Behavior

Total time spent feeding did not vary markedly between males and pregnant females (males = 15%; pregnant females = 15%.) There were clear gender differences between males and pregnant females for parts ingested. Males ate more leaves during this period (Fig. 3.23), whereas females fed more on fruits other than TIFR (Fig. 3.24) and flowers (Fig. 3.25).

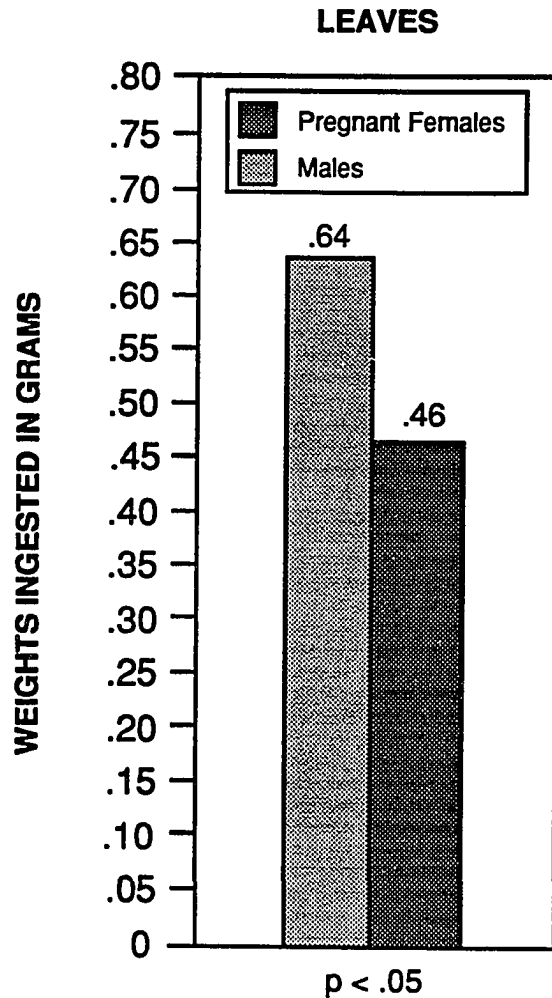


Figure 3.23. Mean Minimum Weights of Leaves Ingested by Males and Pregnant Females.

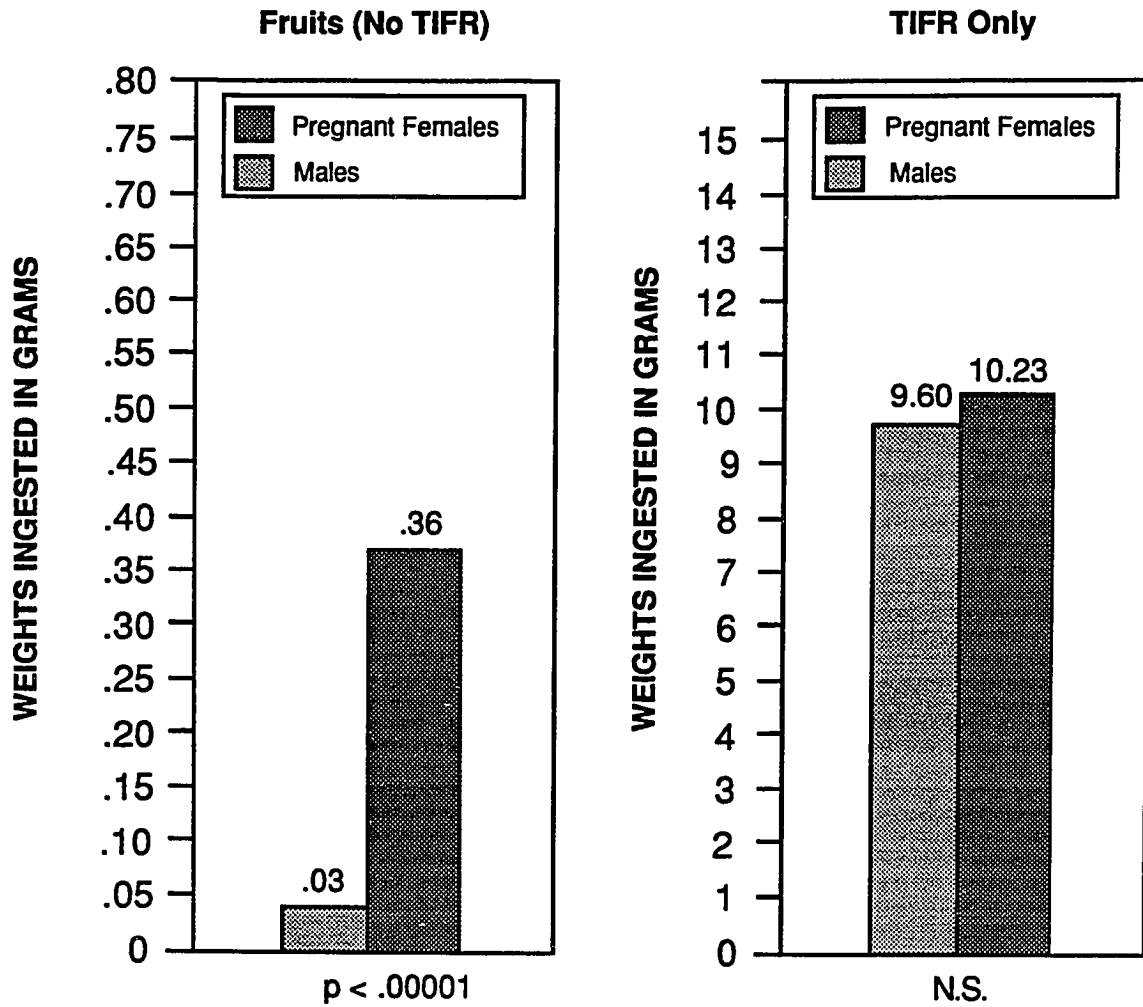


Figure 3.24. Mean Minimum Weights of Fruits Ingested by Males and Pregnant Females.

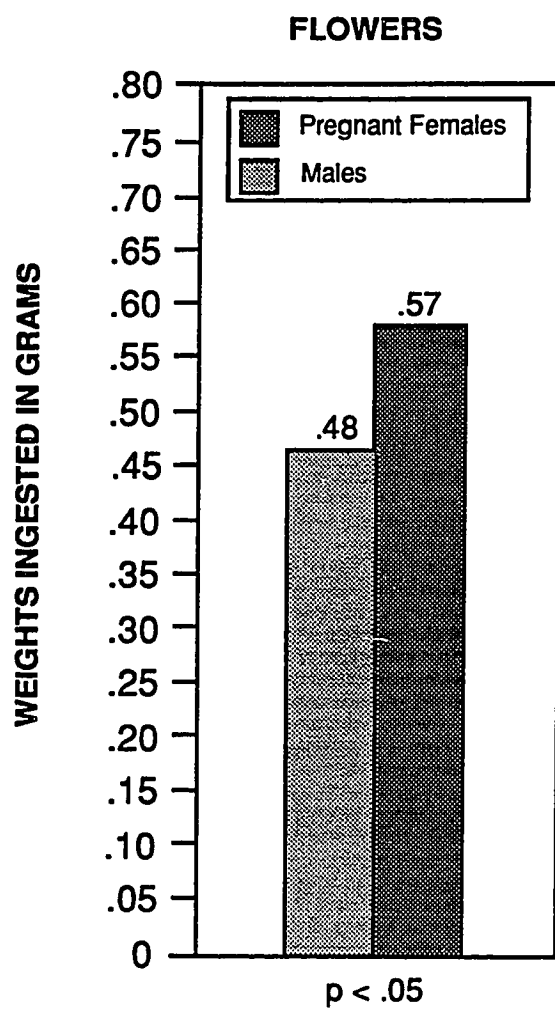


Figure 3.25. Mean minimum weights of flowers ingested by males and pregnant females.

In many species including humans late pregnancy is more energetically demanding, for it is in the third trimester that most growth of the placenta and fetus occurs (Stini, 1988). To give a finer understanding of feeding behavior during this time, the pregnancy period was divided into two periods, early pregnancy (May-June) and late pregnancy (July-August). Males and pregnant females were compared for total time spent feeding, time spent feeding on fruits and flowers.

While there were no important differences between males and pregnant females during either early or late pregnancy for total time spent feeding, pregnant females did feed more on fruits during both early and late pregnancy period (Table 3.13). Pregnant females also fed more on flowers during the late pregnancy periods than did males. Because adult females have priority of access to all foods, these results could reflect female feeding priority and not the nutritional costs of pregnancy *per se*. The proportions of species used during early and late pregnancy are shown in Table 3.14. For each individual an agonistic ratio was then determined for these species and parts. This ratio reflects: total agonistic events over species and part X + total time spent feeding on a species and part X. Numbers greater than 1 reflect more agonism than feeding, and vice versa. The higher the number, the greater the rate of agonism relative to time spent feeding on that species and part. The mean agonistic index for these foods are presented in Table 3.15 for each troop. From the table it is apparent that there is less feeding agonism associated with most flower species when compared to fruit species. Although GAFL shows a high agonistic ratio, males rarely fed on these flowers (see chapter 4). In spite of low feeding agonism associated with flower feeding, males spent less time feeding on most of the flowers (TIFL: males $\bar{x}$ = .11, females $\bar{x}$ = .42; SAFL: Males $\bar{x}$ = .06, females = .94). It is thus possible that higher rates of feeding on flowers by females during late pregnancy and parturition was related to nutritional needs of this reproductive state and not simply an artifact of female feeding priority.

Table 3.13. Comparisons of total time spent feeding, and the mean weights (in grams) of fruits and flowers eaten by males and pregnant females.

	¹ Total Time		² Fruits		TIFR		Flowers	
	Early	Late	Early	Late	Early	Late	Early	Late
Females	12%	20%	.16	.41	6.71	3.00	0	.57
Males	11%	19%	.01	.23	7.69	3.71	0	.48
	n.s.	n.s.	p < .01	p < .05	n.s.	n.s.	n.s.	p < .05

¹ As percentage of all activities.

² Not including TIFR

Table 3.14. Proportions of selected species of fruits and flowers used during the early and late dry season by Black and Green Troop.

Fruits

	ESFR		MFFR		TIFR		SAFR		BEFR		OTHER	
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
BLACK	.13	.33	.01	0	.46	.27	.003	.003	.006	.03	0	.005
GREEN	.06	0	.02	.003	.43	.17	.003	.22	.003	.01	.005	0

Flowers

	QUFL		TIFL		5GFL		GAFL		SAFL	
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
BLACK	0	.16	.02	0	.006	0	0	.006	0	.01
GREEN	0	.22	0	.001	0	.002	0	.02	.002	3

Table 3.15. Mean rates of agonism over species/parts for Green Troop and Black Troop.

Species/Part	BLACK	GREEN
MFFR	.60	1.00
ESFR	.78	.86
QUFL	.22	.24
SAFR	.42	.58
TIFR	.53	.55
GAFL	-	.82
TIFL	.14	.20
5GFL	.25	.13
SAFL	.40	.37
BEFR	.25	.19

There were no marked differences in the number of leaf or fruit species used by males or pregnant females during the dry season (Table 3.16). This is not surprising given the paucity of species available at this time. Furthermore, neither is the fact that both males and pregnant females used more species of leaves than species of fruits because fewer fruits were available in the dry season.

Table 3.16. Comparison of the mean number of fruit and leaf species used by males and by pregnant females during the dry season.

	Fruit Species	Leaf Species	Fruit vs. Leaf Species
Females who lactated	1.30	2.50	p <.02
Females who did not lactate	1.20	2.72	p <.02
Males	1.05	2.82	p <.01
Females who lactated vs females who did not lactate	n.s.	n.s.	
Females who lactated vs males	n.s.	n.s.	
Females who did not lactate vs males	n.s.	n.s.	

Males and pregnant females spent similar amounts of time foraging on fruits (dry season: males = 5%; pregnant females = 6%). Fig. 3.26 compares the efficiency ratios for fruit feeding during the dry season. Males and pregnant females had similar ratios, regardless of whether the female had lactated or not.

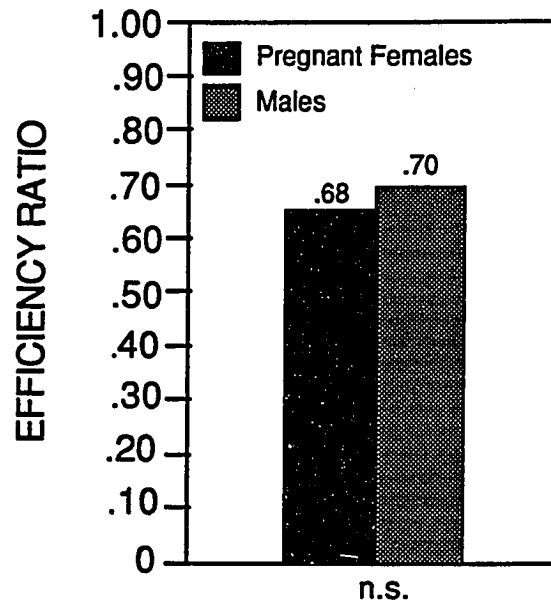


Figure. 3.26. Comparison of Feeding Efficiency on Fruits During the Dry Season between males and pregnant females.

As noted before, males used termite soil more than either class of females during the wet season. This was reversed in the dry season, where pregnant females focused more on this item than did males (Fig. 3.27).

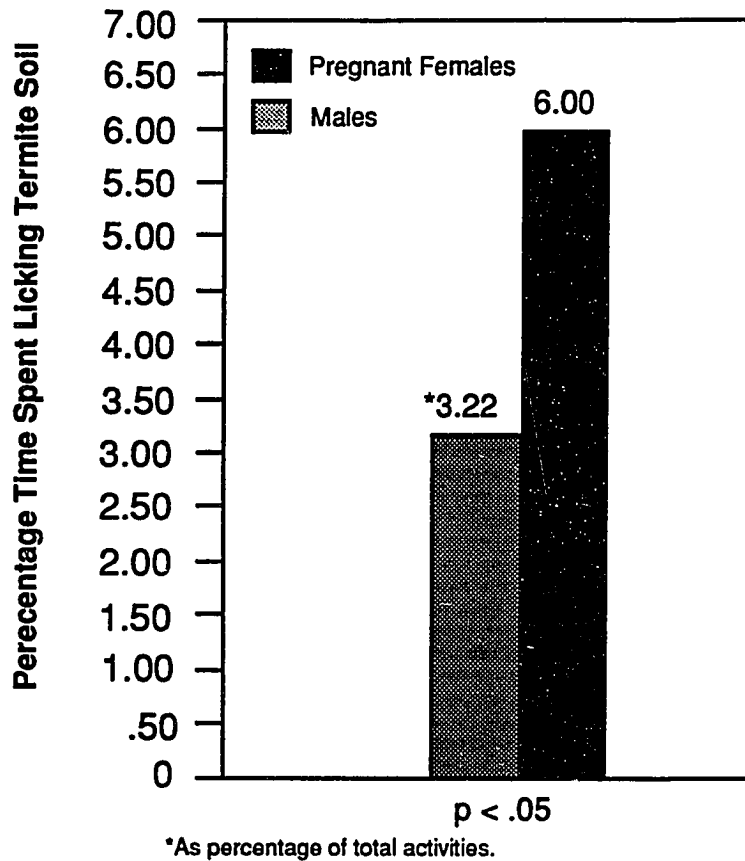


Figure 3.27. Time Spent Feeding and Licking Termite Soil by Pregnant Females and by Males During the Dry Season.

Use of the Environment

Time spent walking or using more active forms of movement at different levels was variable, and no pattern could be discerned. Pregnant females spent more time feeding in the trees than did males, whereas males fed more at ground level (Table 3.17). This is most likely due to pregnant females feeding more on flowers and fruits in the trees, whereas males tended to feed on mature leaves at ground level. Although not significant, males also spent slightly more time licking and ingesting kily fruit at ground level (males = 4.14%, females = 3%).

Table 3.17. Comparisons of the mean percentage of time spent feeding at different levels by pregnant females and by males.

	Ground	Bush	Tree
Pregnant females	17%	13%	70%
Males	31%	15%	54%
Pregnant females vs. Males	$p < .02$	n.s.	$p < .02$

PARTURITION

Time Spent Feeding

During October five females were followed continuously just prior to and for several days after parturition in order to document changes in activity during this period. Four of these females (female 13, 53, 33, and 73) were from Green Troop and one was from Black Troop (female 82). Fig. 3.28 shows the percentage of time spent feeding during this period. Females who kept their infants spent less time feeding during this period than they did three weeks before and (indicated by an "*" in the figure). All females showed a substantial decline in time spent feeding either on the day of parturition (females 13 and 82) or for several days prior and/or after birth (females 53, 33 and 73). Note also the steady increase in time spent feeding after parturition, which continues for three weeks after birth. This pattern occurs for all females except female 82 who lost her infant shortly after birth, and who shows a much more variable feeding pattern after parturition.

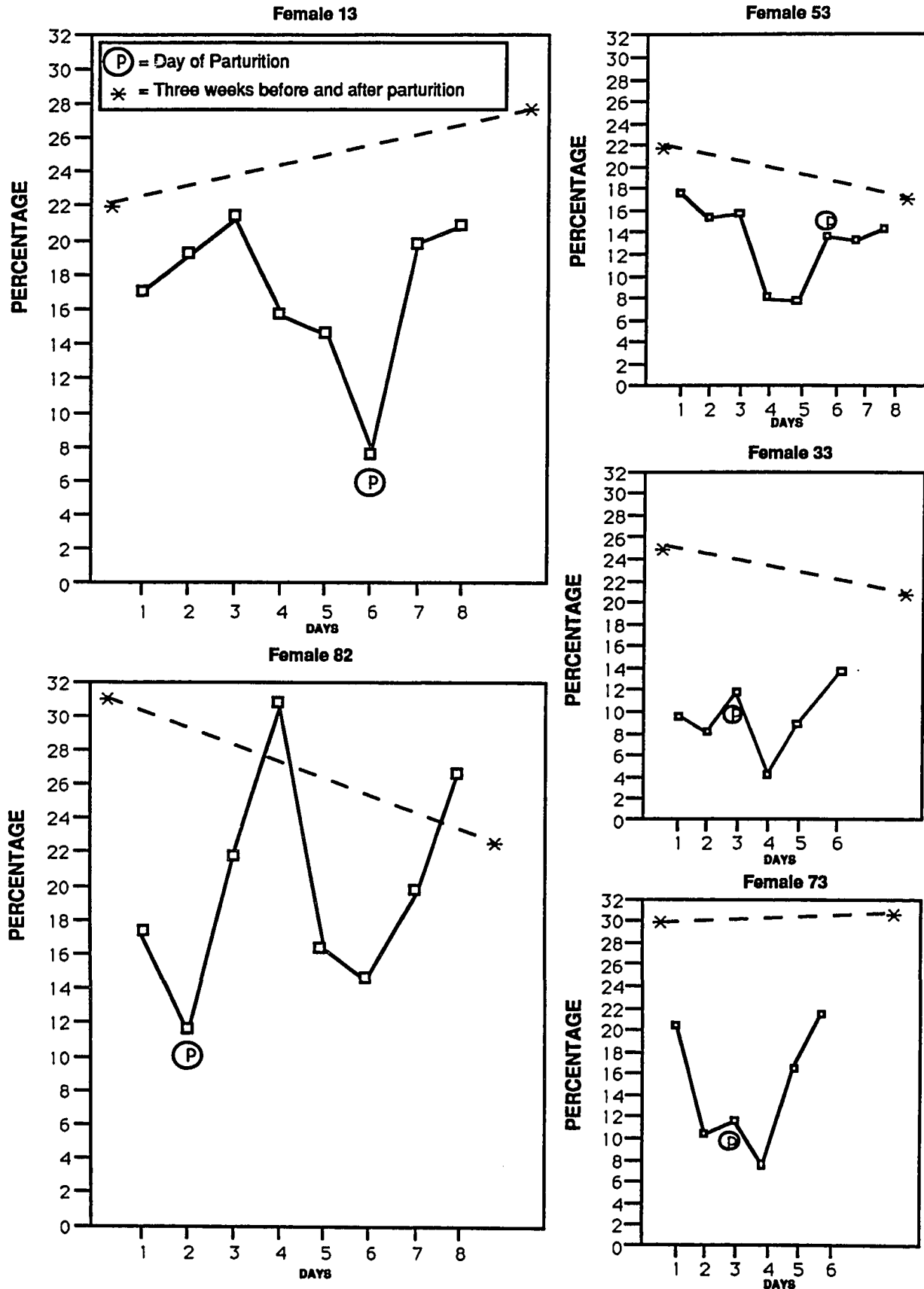


Figure 3.28. Percentage Time Spent Feeding During Birth Season Day Follows.

Fig 3.29 diagrams the percentage of time spent feeding on major food parts during this period. To determine the effects of parturition on feeding behavior percentages of time spent feeding are plotted by day. Females 53, 82, 33, and 73 all had their infants at dusk. Therefore the day after parturition was the first full day of feeding after birth. Female 13, however, had her infant in the morning so her first day of feeding was the actual day of parturition. For four of the five females, a single food type was emphasized on the first full day of feeding (female 13: flowers; females 53 and 73: leaf buds; female 33: licking kily fruit of *T. indica*). Again, female 82, who lost her infant by the next day, does not show such a pattern.

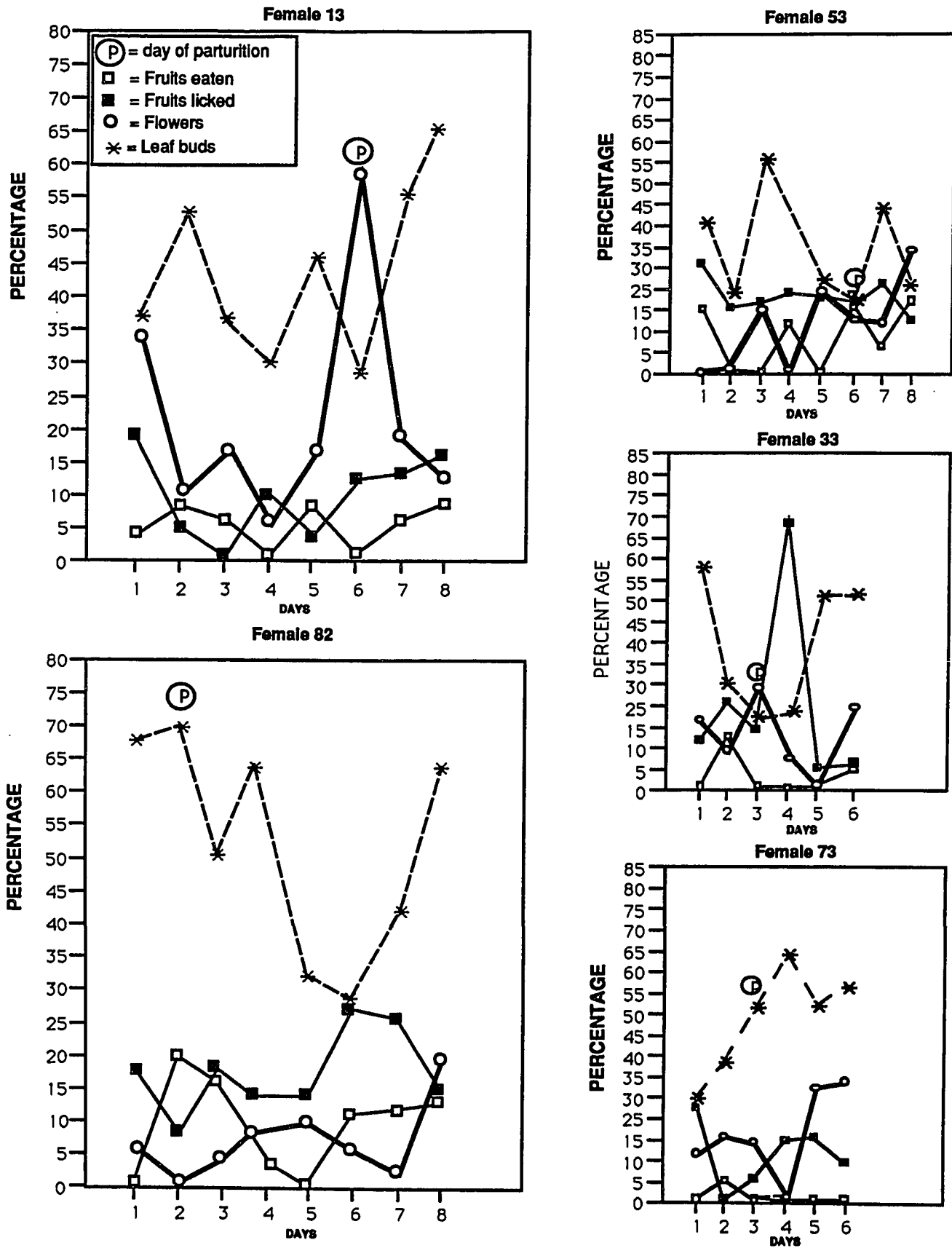


Figure 3.29. Percentage Time Spent Feeding on Major Food Parts During Birth Season Day Follows.

All females focused on leaf buds during this period. However, this is not necessarily attributable to pregnancy and parturition *per se* since female 82 shows the same pattern and she lost her infant immediately after parturition. Time spent feeding on flowers was higher for females who kept their infants, but was markedly lower for the female who lost her infant (female 82, Table 3.18). Since this female was sampled on the same days as female 53 these differences are not attributable to phenological changes and may be related to parturition and early lactation.

Table 3.18. Percentages of time spent feeding on the major food types during day follows prior, during and after parturition.

	Female 13	Female 82 ²	Female 53	Female 33	Female 73
Leaf buds ¹	43%	50%	36%	40%	45%
Flowers	27%	5%	14%	15%	20%
Fruit	19%	22%	27%	29%	21%
Other	11%	23%	23%	16%	14%

¹ Percentage of time spent feeding on leaf buds was higher than any other food type for all females at $p < .05$ for all females.

² This female lost her infant the day after parturition. For this female the percentage of time spent feeding on flowers was markedly less than all other females at $p < .05$.

Fig. 3.30 shows the use of termite soil during this period. For pregnant females, the mean percentage of time spent licking and ingesting termite soil during this period was comparable to mean percentages throughout the dry season (6% during the dry season, 7% during day follows). For all females, use of termite soil peaked either on the day of parturition (female 33) or the day just prior to birth (females 13, 53, 82, and 73).

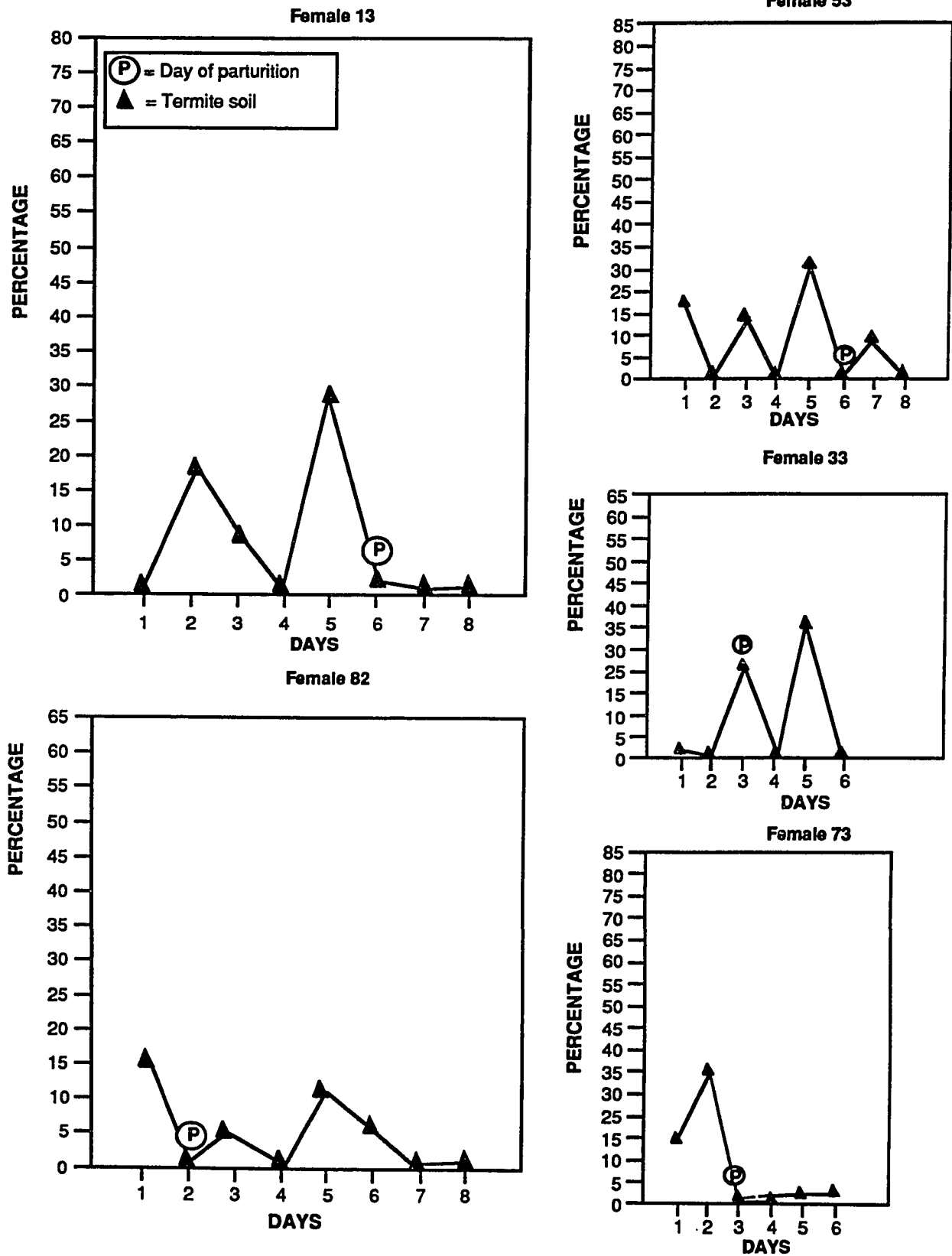


Figure 3.30. Percentage Time Spent Feeding on or Licking Termite Soil During Birth Season Day Follows.

Allogrooming

Allogrooming and autogrooming also changed relative to parturition (Fig. 3.31). Allogrooming increased dramatically on the day of parturition (females 13, 82, 53, 73) or the day after (female 33). Autogrooming also increased for all females. Time spent resting tended to remain low on or during the days prior to parturition

Resting

Time spent resting is shown in Fig. 3.32. Pregnant females maintained or decreased time spent resting on the day of parturition.

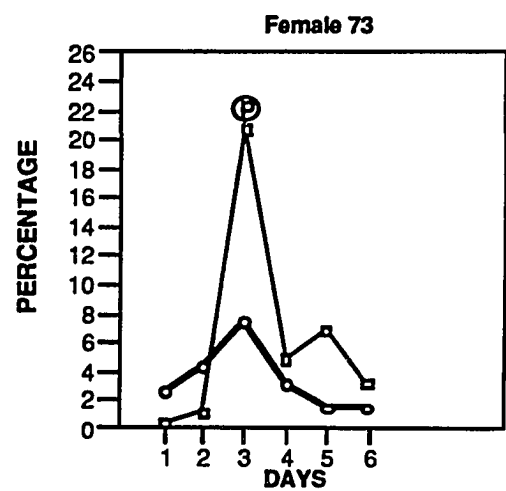
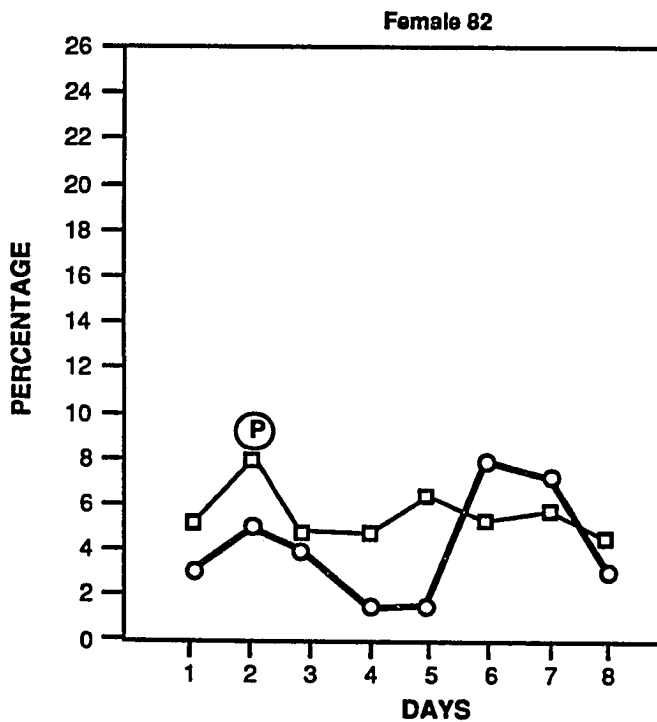
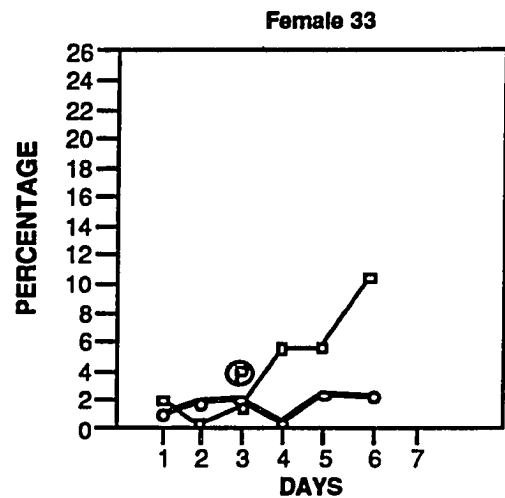
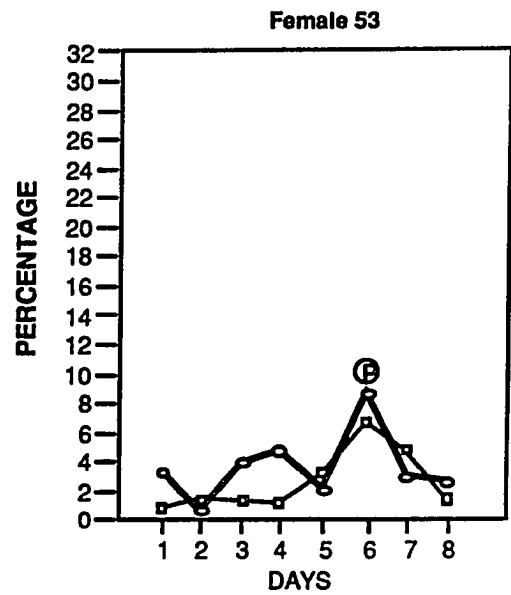
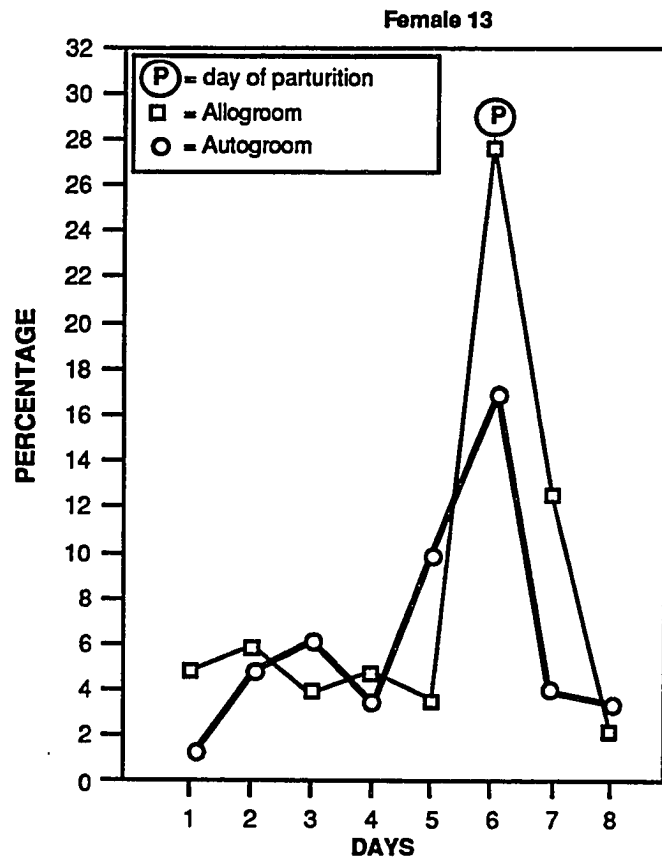


Figure 3.31. Percentage Time Spent Allogrooming and Autogrooming During Birth Season Day Follows.

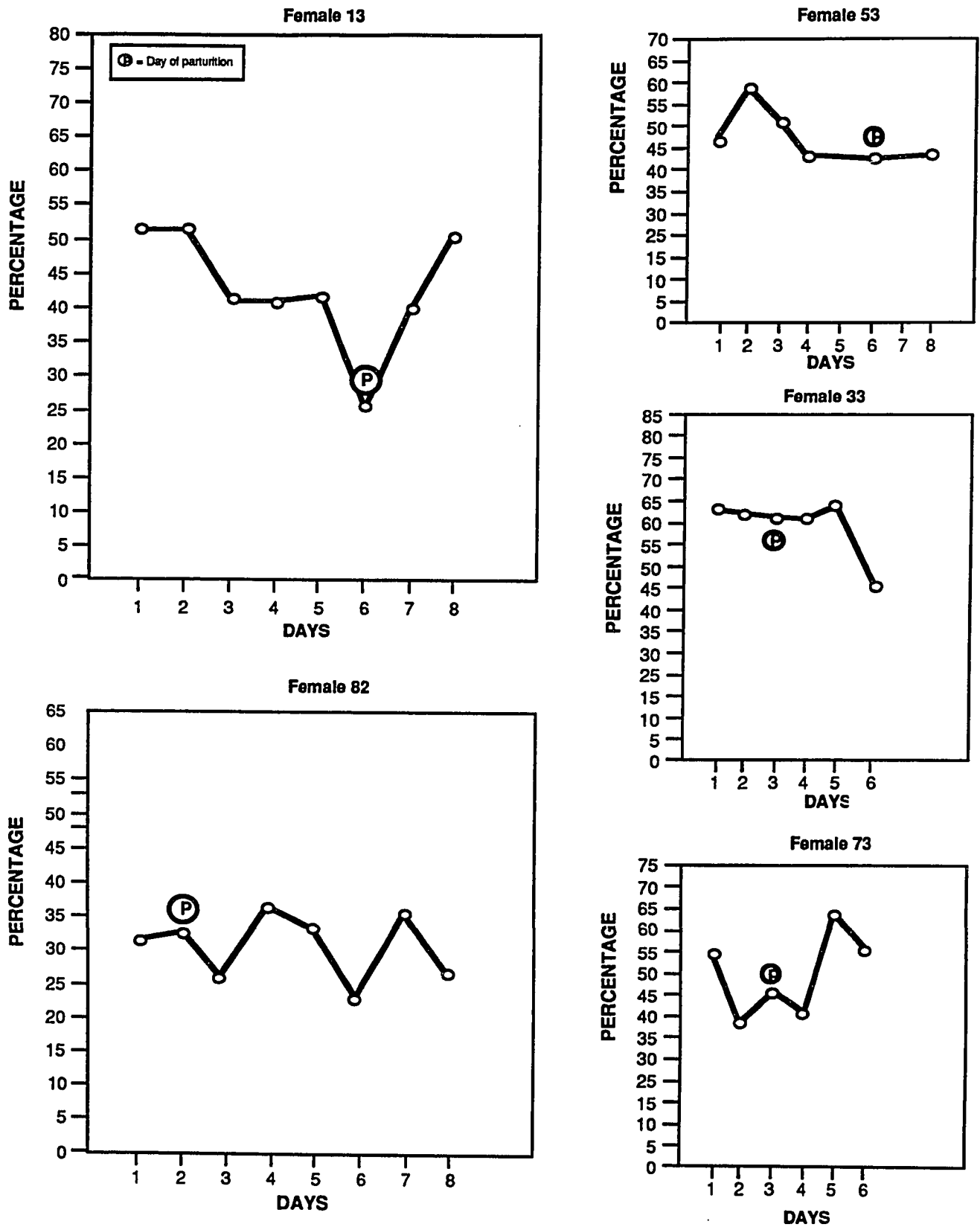


Figure 3.32. Percentage Time Spent Resting During Birth Season Day Follows.

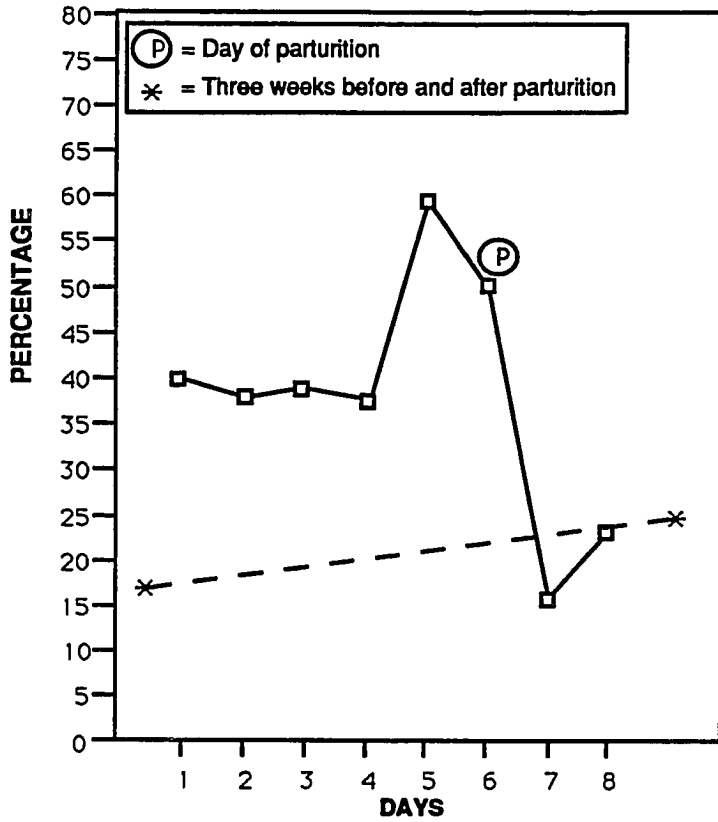
Use of the Environment

During the week of parturition, time spent at ground level was elevated when compared to time spent at this level three weeks before or after parturition, (indicated by an "*" in Fig. 3.33). Again, 82 who lost her infant shows more variability. Time spent at ground level decreased on the day of parturition (females 13, 82, 53, 73) or for several days after (female 33).

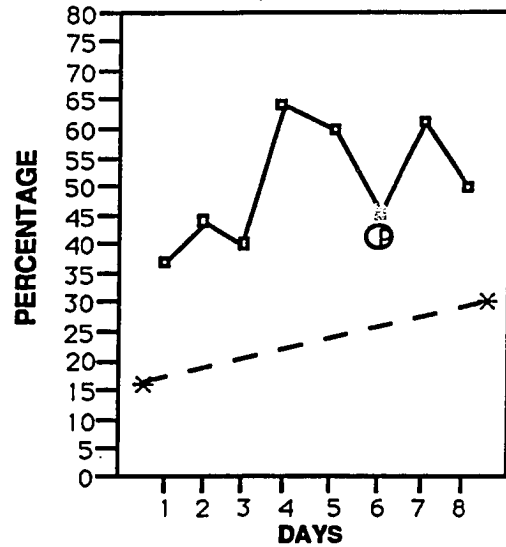
Activity Levels

Fig 3.34 illustrates the percentage of time spent in active and less active movement during birth season day follows. For most females this period is characterized by a higher percentage of time spent walking at ground level. The only exception is female 82, who lost her infant after birth. For this female the period is distinguished by a considerable overlap of the various types of movement. Walking in the trees is also important for three of the four females who retained their infants. The exception was female 13, who was the highest-ranking female in Green Troop. For her there is considerable overlap of other forms of movement at tree level. Relative to other forms of movement and levels, all females spent a high percentage of time walking at ground level on the day of parturition.

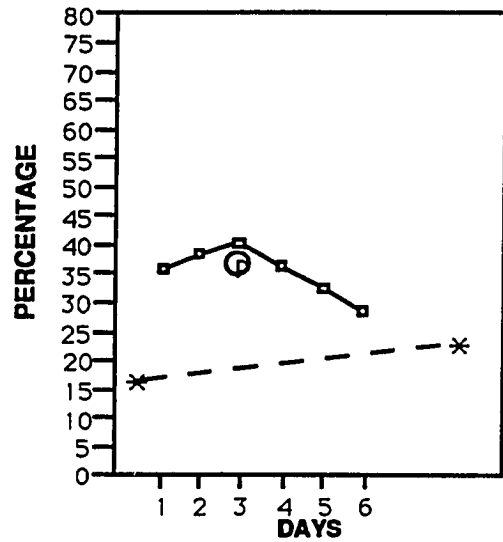
Female 13



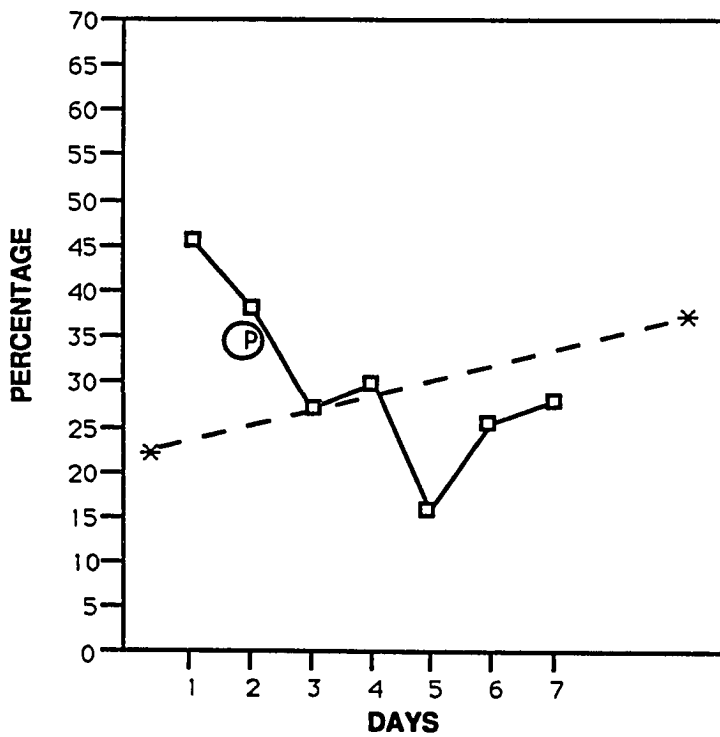
Female 53



Female 33



Female 82



Female 73

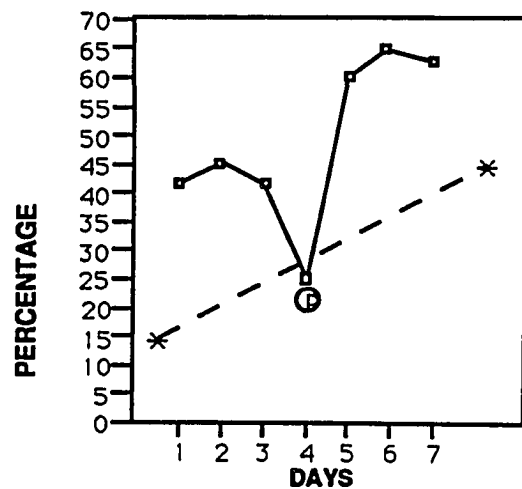


Figure 3.33 Percentage Time Spent on the Ground During Birth Season Day Follows.

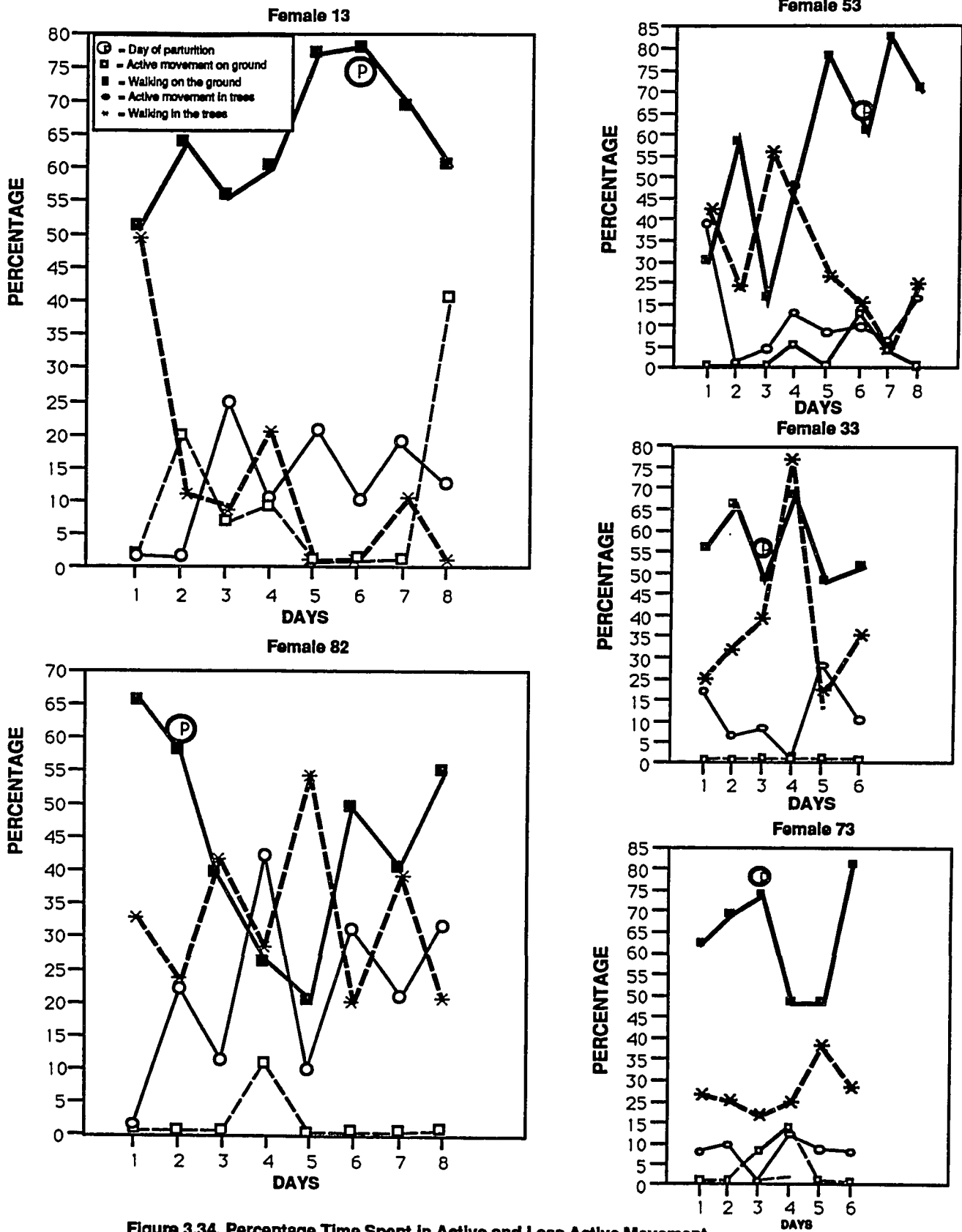


Figure 3.34. Percentage Time Spent in Active and Less Active Movement on the Ground and In the Trees During Birth Season Day Follows.

DISCUSSION

LACTATION: FEEDING AND ACTIVITY PATTERNS

Energy Conservation

At least four behavioral adaptations seem possible to deal with increased demands associated with pregnancy and lactation. First, individuals can reduce their food intake, reduce weight and utilize fat stores (King and Murphy, 1985). Second, they can attempt to reduce dietary requirements by reducing energy expended, e.g. resting more and reducing all other activities, including feeding and hence potential energy expended over feeding competition (Harrison, 1983b). Third, individuals can focus on food types that require less energy to acquire (see below). Fourth, individuals can increase food intake.

Energy storage from one reproductive state to the next is more often found in large mammals (Gittleman and Thompson, 1988). With respect to primates, increased body fat, as determined by bioelectrical impedance analysis, has been correlated with pregnancy in captive pigtail macaques (McFarland, 1991). Body fat was not measured in the field, but it is unlikely that ringtailed lemur females, who are relatively small, were utilizing fat stores to supplement lactation. Both the availability and quality of food were reduced during the dry season, so that pregnant females had to bear the costs of gestation during a period of limited resources. They therefore entered lactation from a period of reduced food availability, decreasing the likelihood of fat storage. Furthermore lactating females did not reduce time spent feeding relative to other classes of individuals. Lactating and pregnant females also did not spend more time feeding, nor did they have greater total intake than males or nonlactating females (see also Chapter 4).

Nursing ringtailed lemurs did appear to use the second and third tactics. Overall, lactating females employed a more energetically conservative feeding strategy. First, they spent more time resting. This was directly associated with nursing because if only time spent resting is compared the

differences disappear. Lactating females also used less active forms of movement when they were at ground level.

Second, the types of foods used by lactating females potentially reduced energy used. Nursing females focused more on leaf buds and young leaves irregardless of location (ground, bush, tree) whereas nonlactating females spent more time feeding on fruits. The relative processing costs, i.e. the amount of energy needed to locate the food, prepare it, and breakdown the nutrients once ingested, that are associated with feeding on immature leaves versus fruits can be quite different. Ringtailed lemurs primarily utilized leaves from herbaceous species or deciduous trees. Of the 41 species of leaves used, 73% were from terrestrial or climbing herbaceous species, 20% were from deciduous shrubs and trees and only 7% were from evergreen species. The herbaceous species often occurred in large, easily located patches. Compared to evergreen species, leaves from deciduous bushes and trees provide a predictable and easily located food source, since the foliage will all be leaf buds, young leaves or mature leaves at the same time. Evergreen species have a mix of leaf stages, requiring more effort to locate choice young leaves among mature ones. Young leaves, in general, are easier to locate than fruits, and the efficiency of foraging on fruits was much lower than for leaves (Table 3.19). Thus individuals spent less time feeding and more time searching for fruits, whereas for leaf feeding they spent more time feeding than foraging.

Table 3.19. Feeding efficiency associated with fruit and leaf eating in Black and Green Troop.

	FRUITS	LEAVES
BLACK TROOP	1.23 ¹	9.56
GREEN TROOP	1.38	17.66

¹ Time spent feeding divided by time spent foraging. The higher the number the more efficient it is to forage on that food item.

Fruit feeding may also be more costly than leaf eating in that it requires more active forms of foraging such as climbing up and down trees and leaping from tree to tree. Leaf feeding is relatively easy as most leaves fed upon during the lactation period were from terrestrial herbaceous species, and in fact lactating females fed more on leaves at ground level or in bushes, and less on fruits in the trees. Fruits were also more expensive in terms of agonism. Agonistic displacements over fruit were much higher than displacements over leaves (Table 3.20).

Table 3.20. Rates of displacement over fruits and leaves in Black and Green troop.

	GREEN TROOP	BLACK TROOP
SAFR ¹	.34 ²	.40
GRFR	.43	.70
PALV	.17	.00
PELV	.00	.00

¹ See Table 2.3 for complete plant names.

² The higher the number the greater the rate of displacement relative to time spent feeding on that food. No displacement is denoted by a 0.

Future analyses of the chemical composition of *L. catta* foods collected in the field will clarify the feeding differences observed. However, utilizing more young leaves than fruits was probably not more costly for lactating females in terms of digestion. While mature leaves are difficult for nonruminants to digest (see below) young leaf buds and leaves are relatively easy to break down, and do not necessarily contain more fiber than fruits (see Barton, 1989; Rogers, 1990). During the wet season *L. catta* utilized only young leaves and leaf buds during leaf feeding. Fruits can also vary in terms of processing costs. Some primate fruits are difficult to access because of hard coverings (e.g. fruits used by *Cebus apella*, Terborgh, 1983; Lucas, 1989), they can vary in fiber content, and unripe fruits can contain higher percentages of

phenolics (Rogers, et al. 1990). Except for the fruit of *T. indica* the fruits used as food by ringtailed lemurs were all small and soft-bodied, some occurring in clusters like grapes (*Talinella dolphinensis*, *Antidesma petiolare*). For fruits that could be clearly divided into ripe and unripe, ripe fruits were selected. Although not measured directly, the digestability of most fruits (except *T. indica*, see below) versus young leaves and leaf buds were probably not very different (see Rogers, et al., 1990). Thus by focusing on immature herbaceous leaves, lactating females were using a food source that potentially cost little to locate, prepare and digest. They were also reducing energy needs by resting more, and by feeding less on fruits which are more costly in terms of foraging.

Feeding Behavior During Lactation.

It was expected that lactating ringtailed lemurs would respond to increased nutritional demands associated with this reproductive state by exhibiting higher levels of time spent feeding. However, there were no marked differences between any classes of individuals for feeding time. Yet, lactating females did show different feeding behaviors with respect to specific types of foods. This suggests that gross categories such as total time spent feeding may have limited value in elucidating interindividual feeding variability.

All mammals require an adequate balance of protein, energy and other nutrients. Fruits and leaves are not mutually exclusive as fruits are generally higher in energy (water-soluble carbohydrates) (Gaulin and Konner, 1977; Rogers, et al., 1990) whereas leaves generally contain higher levels of protein, and other micronutrients (Waterman, et al., 1983; Coley, 1983; Barton, 1989). Access to utilizable nutrients in leaves also vary based on soil condition, leaf type (e.g. herbaceous, evergreen, deciduous) and maturity of leaves. Some forests contain remarkably infertile soil which results in plants with high amounts of digestion-inhibitors even in young leaves (e.g. Douala-Edea: McKey et al. 1978; Gartlan, et al. 1980; Waterman and Choo, 1981). Leaves of herbaceous species tend to be lower in digestion inhibitors and higher in protein and other micronutrients than leaves of trees, especially those that are evergreen (Waterman, et al., 1983; Coley, 1983). Nutrients available in

leaves from deciduous species follow the developmental stages of leaves, with young leaves exhibiting greater amounts of protein and energy (Baranga, 1983). Mature leaves are normally harder to digest because they contain strong cellular walls that are difficult for species without special morphological adaptations for rumination to access (Waterman and Choo, 1981). Young leaves are usually easier to digest and have higher percentages of accessible protein and other micronutrients (Waterman, et al., 1983) because the cellular walls are weaker and can easily be broken down by nonruminants. In some cases mature leaves have also been shown to contain higher percentages of digestion inhibitors such as secondary compounds, whereas immature leaves of the same species contained relatively less of such compounds (Waterman and Choo, 1981, but see Coley, 1983). Leaves are a good source of calcium (Waterman, et al., 1983) and flowers can provide equally high percentages of protein (Gaulin and Konner, 1977). Leaves used by *L. catta* at Beza Mahafaly during the wet/lactating season were mainly from herbaceous species and deciduous trees, and may have been low in both secondary compounds and higher in micronutrients than other evergreen species not utilized. Individuals probably avoided a buildup of any one type of secondary compound by feeding only a short time on a number of leaf species. However, only phytochemical analyses can determine this, and future analyses on collected samples of ringtailed lemur foods should clarify the importance of nutrients and toxins in *L. catta* foods.

Lactating mammals have greater protein and calcium requirements than females of other reproductive states (Widdowson, 1977). Depending on her body size, from the perspective of a lactating nonhuman primate, these needs can best be met by increasing the percentage of young leaves, insects, and/or flowers in her diet. Flower availability was strictly seasonal during the study period, and few flowers were available during the wet/lactating season at Beza Mahafaly. Insect protein, however, was available and utilized by all individuals during November, which coincides with early lactation. During this month caterpillars were eaten (Black Troop: 4%; note that caterpillar feeding was a rare event, and although observed for members of Green Troop, it did not appear in any five minute sample) as were cicada (Black Troop: 7%; Green Troop: 2%). A fair amount of time was also spent foraging

for caterpillars by one of the troops (Black Troop: 11%) and cicada (Black Troop: 18%; Green Troop: 2%).

The wet season was marked by a much higher availability of leaf buds and young leaves (see Table 2.4), and lactating females focused more on these food items than did nonlactating females and males. This follows the general trend for a number of primate species in which lactating females either consume greater amounts or spend more time feeding on protein rich food items, i.e. insects and young leaves (Gautier-Hion, 1980, Harrison, 1983b; Frigaszy, 1986).

Lactating females thus forage and feed differently from other individuals, which is most likely related to nutritional needs associated with lactation. Focusing on leaf buds and young leaves of herbaceous and deciduous species provided lactating ringtailed females with a predictable food source that helped deal with both the problems of energy conservation and increased protein/calcium requirements.

THE MATING SEASON : FEEDING AND ACTIVITY PATTERNS

The effect of mating activities on feeding ecology and activity levels in mammals has rarely been quantified or directly tested (Gittleman and Thompson, 1988). Kenagy (1987) looked at energy consumption associated with mating in golden-mantled ground squirrels (*Spermophilis saturatus*). He reports energy consumption increased only slightly compared to the nonmating period. More often behavioral observations suggest a cost associated with mating (e.g. reduction in body weight, McCullough, 1969; or time spent feeding, McCullough, 1969; Clutton-Brock, et al, 1982b).

In ringtailed lemurs, which are seasonal breeders, females within a single troop all exhibited estrus within a one to two week period (Sauther, 1991). Females came into estrus on separate days and were receptive for only a 24 hour period. Inter-male competition for reproductive access to females is therefore considerable. Males engage in jump fights (Jolly, 1966), and wounds are common (Jolly, 1966, Sauther, 1991). It has been assumed that females

undergo fewer demands at this time (Gittleman and Thompson, 1988). However, in seasonally breeding species such as *L. catta*, energy expenditure may be quite high. Females actively repel the advances of males who solicit copulations before the female is receptive, and she may move rapidly through the trees followed by potential mates when she is receptive. Thus the mating season is characterized by punctuated bouts of intense activity by both males and females, which are associated directly with mating (Sauther, 1991). In general, activity budgets during the days prior and on the day of mating reflect an attempt to conserve energy during this period. Throughout this time, resting was the single most common activity, increasing well over time spent resting one to two weeks before. At the same time, feeding time was reduced. Individuals also reduced social activity, spending less time allogrooming.

Although the sample size is small, it is notable that both the male and the females followed this pattern. It has been postulated that reproductive strategies differ between males and females, with males focusing on behaviors that enhance their chances to breed, whereas female behavior is associated with optimizing feeding opportunities (Trivers, 1972; Wrangham, 1980). In highly seasonal species, such as ringtailed lemurs, behavioral patterns of males and females may converge during the mating season, with reproductive effort of both males and females emphasized at the cost of feeding and social behavior.

In terms of food choice, it seems logical for animals expending high amounts of energy to focus on foods that in turn provide higher levels of energy, and this indeed seemed to be the case for mating ringtailed lemurs. On the day of mating both the male and females focused on fruit eating, specifically *E. pruinosa* and/or the pods of *T. indica* which had fallen to the ground. Both fruits were easily located and fairly abundant in the forest, and were therefore less costly to forage on relative to other fruits. Thus males and females responded to vigorous mating activity by resting as much as possible and focusing on high energy, easily located foods.

Previous descriptions of ring-tail mating behavior (Jolly, 1966, Koyama, 1988, Sauther, 1991) indicate that estrous females are approached by more than one male and that females usually mate with more than one partner (Koyama, 1988; Sauther, 1991). The highest ranking (central) male engages in pre-copulatory guarding, staying close to a female for several days before she becomes receptive (Sauther, 1991). Results from this study indicate that such pairs show highly correlated activity patterns. For general classes of foods there was a close correlation between the two for time spent feeding on fruits and mature and young leaves. Although the actual species of foods consumed were often different, the correspondance became closer as they approached the day of mating. Time spent feeding on the fruits of *T. indica* was remarkably similar. Such close correlation in activity and feeding behavior were most likely due to the male matching his behavior to the female he was following.

PREGNANCY: FEEDING AND ACTIVITY PATTERNS

Relative Costs of Reproduction

Because of the seasonal nature of reproduction in this species, it was possible to compare the same females over lactation or nonlactation and pregnancy periods. Lactating females maintained equally high levels of leaf feeding when they were pregnant, whereas females who had not lactated markedly increased leaf use, moreso than males. Males, and females who had not lactated showed a dramatic decrease in fruit feeding during the dry season, while females who had lactated showed less reduction. Furthermore, females who had lactated fed more on fruits when they were pregnant than either males or pregnant females who had not lactated. All of this suggests a residual effect, i.e. that the relatively higher costs of lactation can carry over into the pregnancy that follows the lactation period. It also indicates that lactating individuals are more conservative in their feeding behavior, maintaining similar amounts of foods in their diet when they gestate. Nonreproducing individuals (males and nonlactating females) exhibit a more variable feeding pattern.

Feeding Behavior During Pregnancy

In general, the costs of gestation are less than for lactation (Sadleir, 1969; Clutton-Brock, 1989) and may explain why some species gestate during times of limited food availability (Gittleman and Thompson, 1988). Pregnancy in ringtailed lemurs occurred in the cool dry season when food availability decreased (Fig 2.4). During this period leaves continued to be an important food source for pregnant females. Flower buds and flowers also became an important resource for pregnant females. Flowers can be a prominent source of protein, and in some species crude protein can be the same in flowers as in young leaves of the same species (Dougall, et al, 1964). Furthermore, flowers can contain greater percentages of protein than mature leaves of the same species (Ganzhorn, 1985). Although few flowers were available during the wet season (Fig. 2.4.), during late pregnancy and parturition (September-October) large flowering trees provided a source of protein. During the same period fewer leaves were available, and these were all mature leaves, many of them highly dessicated. Consequently, leaf feeding decreased. In addition, less fruit was available at this time. Flowers may thus have supplemented the use of leaves and fruits, and provided pregnant females with a higher quality protein source than males.

During the dry season no differences in general foraging efficiency could be found between males or pregnant females, and all individuals spent more time feeding than foraging. Fruit availability was low, relative to the wet season, and all individuals fed less on this food type. Females fed more on fruits, (not including TIFR), during this period than did males. This is most likely due to the interplay between female feeding dominance and the distribution of fruit resources (see also Chapter 4). During the dry season individuals were observed feeding on only five fruit species, *T. indica* (kily), *E. pruinosa*, *Cissus microdonta*, *Catanaregam spinosa*, and *Maeurua filiformis*. Fruits of *E. pruinosa*, *C. spinosa*, and *M. filiformis* were located on single, small, monopolizable trees, and females could easily displace males from these resources. *Cissus microdonta* was a liana found high in trees and did not seem easily predictable, in terms of distribution. Palatable kily pods (TIFR) were widely distributed because this species produces fruits

asynchronously. There were no gender differences for this fruit, as kily pods are large enough to be carried away in the mouth and eaten elsewhere if an individual is displaced from a feeding site.

Overall, the tactics during this period tend to reflect behavioral adaptations of lactating females. In general pregnant females decreased activity by resting and by decreasing social activity. They continued to use higher protein foods such as leaves during early pregnancy and flowers during late pregnancy. Fruits were less available than at the time of lactation, nevertheless pregnant females used more fruits than did males. Females who had lactated and males rested more during the dry season than females who had not lactated. Again, higher rates of resting may be related to residual effects of lactation for females. For the males, higher resting rates may reflect recuperation from the highly demanding mating season which occurs just at the beginning of the dry season (Sauther, 1991).

Parturition

Energy expenditure by pregnant females is often highest just prior to parturition, and costs at this time may effect energy expenditure during lactation (Gittleman and Thompson, 1988). A decrease in feeding behavior and general activity during late pregnancy has been documented in a number of primate species (Beal, 1971; Darby, 1953; Sauther and Nash, 1986; Kohrs, et al. 1976; Altmann, 1980; Kemnitz, et al. 1986; Meder, 1986; Bolser and Savage-Rumbaugh, 1989). Feeding behavior has also been reported to be lower on the day of parturition (Mitani, 1989). Ringtailed lemur females followed this general pattern, with decreased time spent feeding, especially on the day of parturition. Hormonal effects resulting in depression of food intake may be a causal factor (Bielert and Busse, 1983).

Females nearing parturition appeared to minimize energy expended during movement by spending more time walking on the ground and by feeding on easily located and relatively abundant foods. Surprisingly, time spent resting did not increase during this time, and may reflect the heavy feeding and foraging demands associated with late pregnancy-early lactation

in ringtailed lemurs. Time spent feeding during the first few days of lactation show a characteristic increase which continues during the next three weeks. This gradual increase has been noted for many small lactating mammals (Miller, 1975; Kemnitz, et al. 1986; Sauther and Nash, 1986) and may relate to the heavy demands of milk production required by fast growing neonates. This can be expected to be especially high for ringtailed lemurs who produce active, precocial infants.

The increased time spent autogrooming on the day of parturition may simply be a reflection of imminent labor. Time spent grooming with other conspecifics actually increased on the day of parturition, which was unexpected. Numerous primate species have been reported to become less social as parturition nears (Shively and Mitchell, 1986a, b; Meder, 1986). The most likely explanation is that new mothers were being approached by other conspecifics who were attracted to the neonates, and they were attempting to establish close contact with infants by allogrooming with mothers. On many occasions a mother and another conspecific would allogroom and eventually the conspecific would be licking the infant.

Time spent at ground level decreased either on the day of parturition or for several days after, and may relate to potential predation. During this period, encounters with avian predators peaked, and newborn *L. catta* infants might be especially vulnerable to predation at this time (see Sauther, 1989).

INGESTION OF SOIL FROM TERMITE MOUNDS

Tannins, Tamarinds and Termite Soil

Ringtailed lemurs at Beza Mahafaly did not actually ingest termites, but they often licked or fed on termite "soil" (i.e. soil, termite saliva and excreta used to construct nests). Samples of this soil were collected and will be analyzed in the near future. Soil ingestion or "geophagy" has been documented in other primate species, primarily rhesus macaques (Puget, 1971; Marriot, 1978; Teas et al, 1980; Malik and Southwick, 1988). However,

the use of the term soil or earth may be a misnomer, since most documented reports indicate that primates selectively ingest termite mounds, which varies chemically from other soil (Wood and Sands, 1978).

Lindburg (1977) reports that free-ranging rhesus monkeys (*Macaca mulatta*) ingested soil from termite mounds. Samples of this soil were high in iron. Chimpanzees also fed daily on soil from termites mounds and chimneys (Hladik 1977a). Analysis of this soil revealed that it was also high in iron. Hladik (1977c) also documented ingestion of soil from a termite mound by two species of free-ranging langurs (*Presbytis senex*, *P. entellus*). Mineral content, by dry weight, again indicated the presence of trace amounts of minerals, but only iron was present in high amounts. Hladik (1977a,b) has thus argued that geophagy does not seem to relate to mineral intake, as higher amounts of minerals can be acquired from eating leaves and some fruits. He suggests that ingesting phyllitous soil may help aid digestion by helping to absorb secondary compounds such as tannins. This has yet to be directly tested, but may in fact be the case in ringtailed lemurs.

L. catta at Beza Mahafaly regularly ingested the fruit of *T. indica*, especially during the dry season (May-September). Leaf buds, young leaves and flowers were also eaten, but at very low percentages. Mature leaves of this species were not ingested. Tannins, which are present in the fruit, leaves, and especially the seeds of the kily (Watt and Breyer-Brandwijk, 1962) prevent the absorption of iron, protein and minerals (Choo, et al., 1981). *L. catta* did appear to minimize tannins from kily in that they avoided mature leaves (which often have higher percentages of secondary compounds, Waterman and Choo, 1981), eating only young leaves and especially leaf buds. Ringtailed lemurs also do not eat the seed, but pass it through undigested (Sauther, pers. obs.). Nevertheless, by ingesting some kily per day they were also being exposed, on a daily basis, to their tannins.

Spelman, et al., (1989) have pointed out the prevalence of hemosiderosis (excessive tissue iron deposits) in captive lemurs, including ringtailed lemurs. They suggest that because some species of free-ranging lemurs commonly use foods high in tannins, which prevent the absorption of iron,

these species may either have greater efficiency in absorbing iron, or be adapted to utilizing lower amounts of iron. In captivity lemurs are often given diets high in iron, high in ascorbic acid and low in tannins and hemosiderosis results (Spelman, et al. 1989).

The daily ingestion of termite soil could be advantageous to ringtailed lemurs in three ways. First, if Hladik's premise is correct, then eating the soil may lessen the effect of daily doses of tannins. Second, the one mineral that is represented in high amounts in termite soil is iron (see above). If the termite soil at Beza Mahafaly follows this trend, it is probably high in iron as well. Thus, a daily ingestion of termite soil provides extra iron to help counteract the limiting effects of tannin. Finally, although leaves may contain as high or higher concentrations of minerals, it is not clear how much is available to the individual animal due to secondary compounds normally contained in leaves. Ingesting termite soil possibly provides a "cost-free" source of minerals. This may be especially important to reproducing individuals (see below).

Sex Differences in Termite Soil Consumption

At Beza Mahafaly there were sex differences in termite soil consumption. During the wet season males utilized this resource more than lactating and nonlactating females. Lactating females used less of this item than any other class. If the ingestion of termite soil helps mitigate the effects of tannins in kily fruit (see above), lactating females may have fed less on termite soil during this period because they spent less time feeding on kily fruits. Both males and nonlactating females fed more on kily during this period and they also spent more time using termite soil. A positive correlation between time spent feeding on the fruit of *T. indica* and time spent licking or ingestion termite soil gives some support for this ($R = +.58$; $p < .04$).

During the dry season, the pattern reversed; pregnant females spent more time eating or licking termite soil. Requirements for sodium increase during pregnancy (Pike and Yao, 1971; Hytten and Leitch, 1971) and physiological mechanisms such as increased taste tolerance to higher concentrations of salt

may help insure adequate sodium intake during pregnancy (Brown and Toma, 1986). Termite soil contains sodium (Hladik, 1977a,c), whereas sodium is on average very low in East African browse and pasturage (Dougall, et al, 1964). The nutritional content of ringtailed lemur foods will be analyzed in the future, but many of the same genera were analyzed by Dougall, et al, and they were lower in sodium than the recommended .15 percent dry matter. Calcium salts also accumulate in termite mounds, and soils which have been modified by termites consistently have higher concentrations of calcium, relative to nearby soils (Wood and Sands, 1978). It is notable that large termite mounds are used as salt-licks by free-ranging elephants (Weir, 1972). Pregnant females may thus be attending to increased sodium, iron and calcium requirements by spending more time ingesting/licking termite soil.

SEX DIFFERENCES IN FEEDING ECOLOGY

Female Feeding Priority and Male Reproductive Strategies

Comparing males and females during the wet season, the general pattern to be expected was for males and nonlactating female's feeding behavior to be more similar, because males do not incur the costs of lactation and infant transport. However, this was not borne out, as males behaved more like lactating females for many measures. Although lactating females spent more time feeding on leaves than males, males did feed more on leaves than did nonlactating females. They also used a similar number of leaf species, males used more leaf species than fruit species, and they used the environment in similar ways, spending more time feeding at ground level or in bushes.

I have argued that lactating female's feeding behavior conserves energy while providing for their increased protein and micronutrient requirements. Male ringtailed lemur feeding behavior during this period may be regulated by two factors, 1) female priority of access to food and 2) male reproductive strategies. Males did spend more time feeding on leaves, which are more abundant and are associated with fewer feeding displacements than fruits or flowers. Female feeding priority certainly was a factor affecting male feeding behavior. Females would not hesitate to chase males from a feeding site, and

retribution for a slow responding male could be quick and violent. 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. Usually males quickly left trees that females entered, or males would wait patiently for females to finish in a feeding patch and then feed there themselves.

Given female feeding priority it was surprising that during the wet season feeding efficiency on fruit was higher for males. Efficiency could reflect the individual 1) being less selective (i.e. choosing foods based on their availability rather than other factors such as ripeness) and 2) focusing on foods that require less foraging, i.e. foods that are easier to locate or are associated with fewer feeding displacements. There was no pattern to ripe fruit feeding and there was no evidence that males, per se, were choosing more or less ripe fruits. Males may have fed more efficiently by focusing on a less contested fruit. There is evidence that males were focusing on fruits that were associated with fewer direct foraging costs. Males fed more efficiently on *T. indica* fruit than did females, and they spent more time feeding on this fruit at ground level. This fruit was associated with relatively fewer agonistic displacements (see Table 4.24).

While it is likely that male feeding behavior is responding to female feeding priority, some of the patterns may be explained by male reproductive strategies. In ringtailed lemurs, who are seasonal breeders, females within a single troop all exhibit estrus within a one to two week period (Sauther, 1991). Females come into estrus on separate days and are receptive for only a 24 hour period. Mating competition is therefore intense, and males are required to expend a considerable amount of energy over a very short period (4-5 hours) fighting with other males over any single estrous female. In this species, males attempt to monitor female sexual condition by approaching a female, smelling her ano-genital region and establishing whether she is behaviorally receptive. If a female is not receptive she cuffs the male away. Since a female can become behaviorally receptive at any time, males must continuously monitor troop females and must therefore know where each female is. Sexual monitoring potentially increases a male's chance of being the first to mate, which may be a reproductive advantage (Sauther, 1991,

Pereira and Weiss, 1991). Males can become distraught if they lose sight of females during this period. One male's response to losing sight of a female was to cease feeding and call and search frantically for her. Upon relocating her he rushed up, monitored her, she promptly cuffed him on the nose and he then fed nearby. Fruit feeding, aside from kily feeding on the ground, normally requires more foraging time relative to feeding on leaves (Table 3.19) and occurs primarily in trees, which is less conducive for monitoring females. Leaves, however, are both more abundant and easier to locate, and most leaf feeding was done in bushes or on the ground. Males were thus focusing on low cost, less contested fruits (e.g. *T. indicus*) and leaves. Not only did this potentially reduce feeding displacements from females, it was conducive to successful sexual monitoring of females nearing estrus. Indeed, the male who was continuously followed during the mating season showed just such a pattern of feeding more on leaves.

ACTIVITY BUDGETS AND REPRODUCTION

As already noted, Dunbar and Dunbar (1988) have argued that lactating females should increase resting time rather than decrease social activities as an adaptation to increased feeding requirements, whereas Altmann (1980) suggests that social activities may be curtailed. Unlike geladas, lactating ringtailed lemurs did not exhibit a monthly increase in time spent feeding as their infants matured. Feeding time was very similar for all classes of individuals. All classes fed more at the cost of resting. In addition, lactating and nonlactating females reduced allogrooming when feeding increased. Percent of time spent in social activities such as allogrooming was low (wet season: Black troop = 1.8%; Green troop = 2%; dry season: Black troop = 1%, Green troop = 1.66%), and ringtailed lemur social organization may be such that reducing social activities does not handicap female's relationships with one another, especially since coalitions are mainly between mother-offspring pairs (Taylor, 1986). In geladas, on the other hand, coalitions are maintained and enhanced by grooming activity (Dunbar, 1980, 1984) and social time may be more "valuable" (Dunbar and Dunbar, 1989).

MATERNAL INVESTMENT AND FEEDING ECOLOGY IN RINGTAILED LEMURS

Female social dominance is found in a number of species of Malagasy lemurs, and has been tied to exceedingly high costs of reproduction which require that females have priority of access to all food sources (Jolly, 1984, Young et al, 1990). Specifically, these species combine low basal metabolic rates with high prenatal maternal investment (Young, et al, 1990), and they produce altricial neonates which must then be supported by the mother during their neonate's rapid postnatal growth period (Jolly, 1984). One likely consequence of this rapid growth is a particularly high proportion of energy being obtained from protein in lemur milk, which averages 19% and which is among the highest for primates (Buss et al, 1976). Young, et al, 1990 have pointed out that altricial neonates are also produced by *Lorisiformes* who are not female dominant, and this therefore cannot explain female social dominance, *per se*. However, the *Lorisiformes* potentially lessen these effects because they are solitary foragers, and they characteristically keep their infants in nests, or park their infants during feeding (Bearder, 1987). Diurnal lemur species, especially those living in arid, seasonal environments, potentially encounter more post-natal reproductive stress. They also produce altricial infants, but they carry their infants with them from birth. Furthermore they are social foragers who live in relatively large troops. In addition they also produce more neonatal weight per day of gestation relative to the *Lorisiformes* (Young, et al., 1990). Hence both gestation and lactation may be especially stressful in the social living, diurnal Malagasy lemurs. Two aspects to this argument seem critical as additional causes of stress, and yet have not been investigated in diurnal lemur species. These are resource and reproductive seasonality.

Resource Seasonality

Lancaster and Lee (1965) in a discussion of seasonal reproduction in primates made the inciteful prediction that "It may be that a wide variety of patterns have evolved depending on the lengths of gestation and lactation and the particular ecological complex in which each species or even subspecies lives" p.504. In a study of the feeding strategies of five nocturnal

prosimian species living in the Marasalaza forest of western Madagascar Hladik, et al, (1980) noted seasonal variations in flower, fruit and leaf production similar to that observed at Beza Mahafaly. Flower production peaked in October and November, and fruits were abundant during the weaning period for young lemurs. Births occurred for *Chierogaleus medius* in January, when food availability was relatively high.

While it is reasonable to assume that diurnal lemur species who gestate and give birth during the dry season have decreased availability of resources (Jolly, 1984) this has not been measured against actual phenological availability. Fig. 3.35 depicts ringtailed lemur reproductive events relative to the mean phenological availability of food parts and seasonal rainfall at Beza Mahafaly. This pattern suggests several stress points, that can be behaviorally mediated. First, females gestate during periods of low food availability. In this study females adapted to this period by resting more, decreasing other activities, and feeding on foods which minimize agonistic displacement. A second stress point is during the mating season in May. During this period daily temperatures were still high ($\bar{x} = 32.2$ c. for May), and food availability decreased. Mating individuals attempted to adapt by reducing overall activities, including feeding and by resting more. Lactation occurs during the period of relative food abundance, but females enter lactation from a period of reduced food availability, limiting their ability to store fat. Thus early lactation, when females must support fast-growing precocial infants, may also be a stressful period. Weaning, however, begins during the peak of food abundance (February). Ringtailed lemur females thus face discrete periods of food stress associated with specific reproductive events.

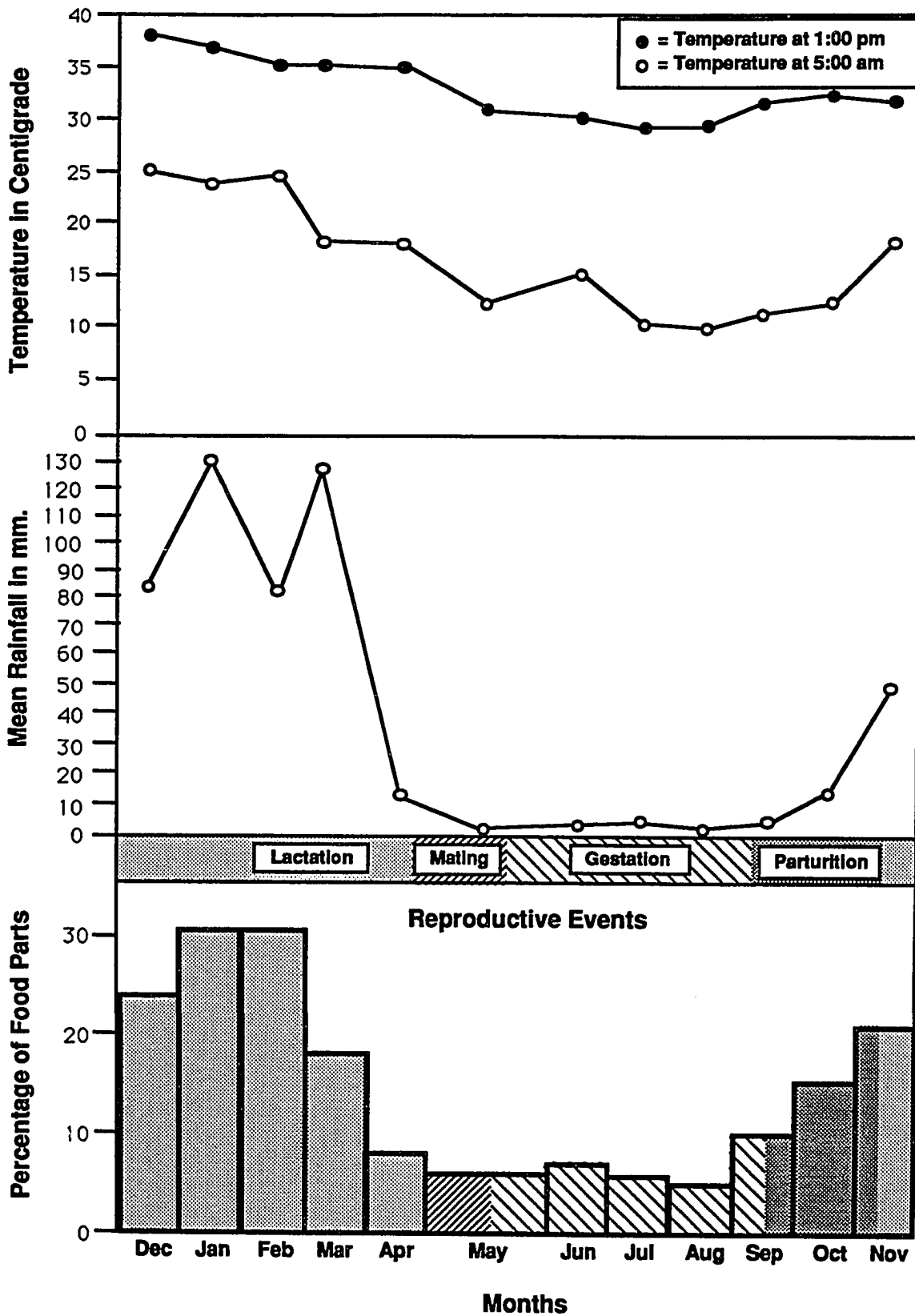


Figure 3.35. Temperature, Rainfall, Mean Percentage of Monthly Phenological Samples Containing Food Parts, and *Lemur catta* Reproductive Events.

Reproductive Seasonality

Reproductive seasonality has both advantages and disadvantages. Izard (1991) has suggested that estrus synchrony in lemurs may reduce potential predation by swamping predators with large numbers of infants, and may provide social advantages (infants will have similarly aged playmates; maternal care can be shared by close kin). Another, and perhaps more critical advantage, is that synchrony allows females (and their infants) to exploit seasonally available resources. Figure 3.36 depicts the availability of food parts relative to reproductive events. In ringtailed lemurs studied at Beza Mahafaly, females lactated when resource were relatively abundant. Furthermore, they began weaning their infants in February and March, when weaning foods that were easy to locate and process, such as young leaf buds of *T. indica*, peaked in availability. In addition, females gave birth and entered lactation when flowers of *Quisivianthe papinae*; *Gyrocarpus americanus* and *Salvadora augsifolia* all became available.

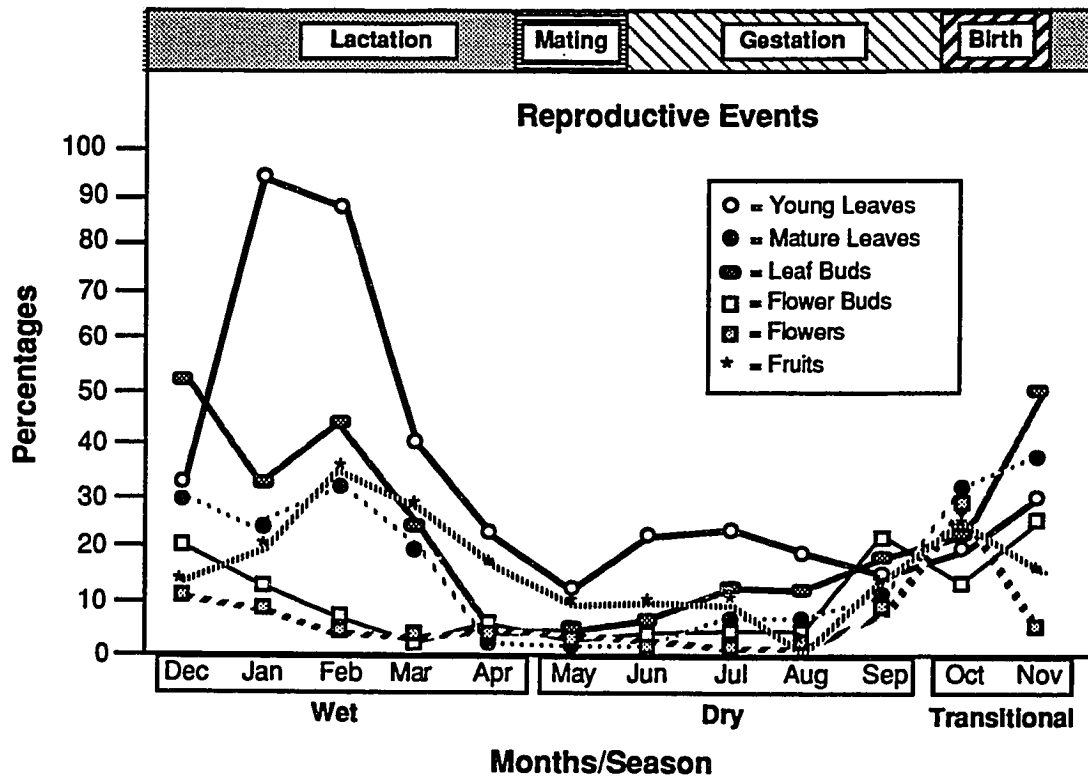


Figure 3.36. Monthly Percentage of Phenology Trees Exhibiting the Presence of Plant Parts Relative to Reproductive State In Ringtailed Lemurs

However, in addition to stresses imposed by resource seasonality, reproductive seasonality can create additional feeding constraints. Individual ringtailed lemurs exhibit one of the most highly constrained mating seasons, approximately 24 hours, (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, 1991). This means that breeding females in a troop will experience identical critical reproductive events, and undergo similar reproductive stresses which could lead to heavy interindividual resource competition. Under such conditions, extra feeding competition from troop males would be a distinct disadvantage to females unless they had feeding priority, and female dominance may develop under such conditions to mitigate male resource competition. The role of competition will be more fully explored in Chapters 4 and 5. Furthermore, such reproductive

seasonality could also have disastrous consequences during years of reduced rainfall, which does occur periodically at this site. During such periods *T. indica* may become especially important as it produces fruit asynchronously and is thus available all year. It is also possible that ringtailed lemurs adjust their mating season relative to rainfall and hence availability of resources, but this has not been investigated in the field.

Finally, Martin (1975) originally made the suggestion that short gestation lengths in the lemuriforms might be considered a modification of r-selected reproduction to deal with highly seasonal environments (see also Rowell, 1977; 1979; Young, et al., 1990). In this vein, one final source of stress seems important in addressing the issue of female social dominance and maternal investment, and that is the inter-birth interval. Demographic evidence suggest that ringtailed lemurs may not only face costly reproduction during periodic food scarcity, but may do so on a yearly basis. At Beza Mahafaly, 80% or more of the breeding females have given birth in two consecutive years (Sussman, 1991), and multiparous females in Green and Black Troop have produced infants three years in a row.

Reproduction in ringtailed lemurs thus shows a unique combination of high pre- and post-natal maternal investment that is set against a highly seasonal resource base. All of these factors may combine to create exceptionally high reproductive costs which are then mitigated by female feeding priority.

CHAPTER 4

INTRAGROUP CONTEST COMPETITION

INTRODUCTION

Competition for resources as a natural by-product of group-living is an old premise, dating back at least to Malthus, who observed that population size increased geometrically, but resources only arithmetically (1809). Yet it is only in the last decade that primatologists have begun to focus on the dynamics of resource competition as a means of understanding key issues such as primate sociality and reproductive success.

A recent body of primate literature has sought the ecological basis for group living by focusing on female requirements (Wrangham, 1980, Van Schaik, 1989, Isbell, 1991). Females incur higher reproductive costs, (Sadleir 1969) which translates into greater nutritional requirements. Hence an important question has been why do most female primates live in groups when group living has been associated with increased feeding competition (Alexander, 1974)?

As summarized by Janson and van Schaik (1988) there are four types of resource competition that can occur in social living species. Intra-group competition includes "contest" competition where individuals directly affect each other's feeding behavior by displacements from a food patch, food stealing, etc. It also includes "scramble" competition which occurs when some food patches are depleted by individuals before others can utilize them. Intergroup competition also occurs and can be of the contest type where different groups compete for access to food patches, or the scramble variety where the groups indirectly affect one another by depleting patches.

Wrangham (1980) proposed that because resources are more directly important to female reproductive success, "female-bonded" groups develop in order to defend important food patches from other groups. Females defend resources from other female groups only when they are clumped in

space. Intragroup competition is offset by the advantages of inter-group resource competition, and is expected only when resources vary qualitatively so that it is advantageous to compete for high-quality foods.

A major drawback in the Wrangham model is that it does not account for why nonfemale-bonded primate species also live in groups (van Schaik, 1989). Van Schaik (1989) expanded Wrangham's model to incorporate the idea that optimal group size is a balance between predation pressure, which encourages larger group size, and intragroup feeding competition, which promotes smaller group size (see also van Schaik and van Hoof, 1983; Terborgh, 1983; Terborgh and Janson 1986). In this model predation pressure alone is the driving force in female group formation, with a causal relationship between predation pressure, larger groups, greater feeding competition, and strong, well delineated female dominance hierarchies. Intergroup competition, so critical to Wrangham's model, is viewed as important only under special circumstances where predation pressure is lessened, either due to characteristics of the primate species or in oceanic island species due to the proposed absence or reduction of important predators.

Most recently, Isbell (1991) has utilized a large body of published primate data on intragroup dominance hierarchies, female agonism, and the interplay between group size, home range, day-range length, and reproductive rates to produce a model which supports Wrangham's theory, but which emphasizes food resources as the prime determinant of inter- and intragroup feeding competition. In her model the distribution of resources, clumped or dispersed, determine intragroup competition, but food abundance is correlated with inter-group competition. Unlike Van Schaik's model (1989) predation is not a necessary element for explaining female relationships.

The focus of the next two chapters is to explore the dynamics of resource competition in ringtailed lemurs. In this chapter the nature of rank-related differences in feeding behavior and efficiency in a female dominant species will be presented with a focus on intragroup contest competition. In the following chapter inter-group contest competition and social group size effects will be explored.

RESULTS

NEAREST NEIGHBORS

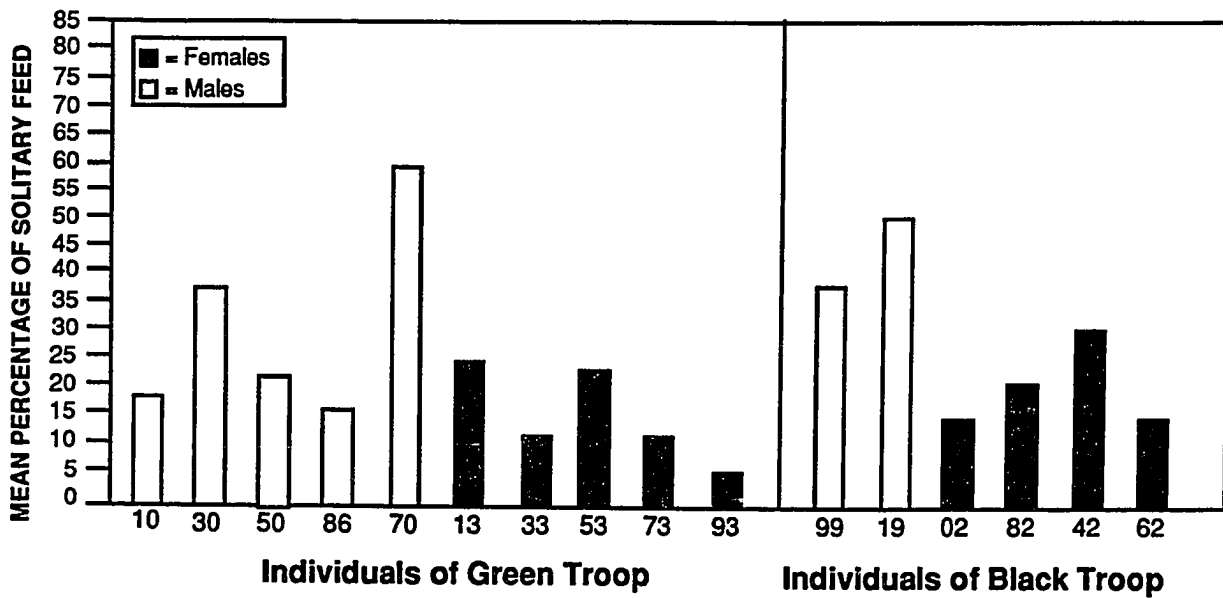
One potential source of feeding competition is having close nearest neighbors during feeding bouts. Spatial relationships during feeding can presumably affect feeding efficiency, and close neighbors could limit resource use. Close neighbors could be costly to high ranking individuals, in terms of energy expended to displace others from feeding sites. Lower-ranking individuals would also be impacted by feeding near higher-ranking members. Furthermore, the availability of resources could be reduced if individuals fed closely to one another, especially for limited resources such as seasonal fruits or flowers. In addition, individuals with similar dietary needs might avoid feeding near one another (Robinson, 1981).

To determine the spatial relationship between feeding or foraging members, the behavior of a focal animals' nearest neighbor was recorded each 15 minutes. In the following sections, data are presented only for nearest neighbors who were also feeding or foraging.

Solitary Feeding

Individuals whose nearest neighbor were 8 meters or more away were scored as "solitary feeding" (Figure 4.1). During the wet season there were no clear rank effects within each gender associated with solitary feeding. However, both males (Black Troop: 19, 99; Green Troop: 10, 30, 50, 86, 70) and lactating females (Black Troop: 82, 42; Green Troop: 13, 53) spent markedly more time in solitary feeding than did nonlactating females ($p < .05$). This might at first seem surprising due to the potential for predation on young infants (Sauther, 1989). In Fig. 4.2 the percentage of solitary feeding is plotted by month for all females. In both troops lactating females spent the greatest time feeding alone in December, when infants were still spending most of their time on the mother, and when predation pressure, as measured by sightings of potential predators, was lower than during the birth or weaning period (see Sauther, 1989).

Solitary Feeding (Nearest Neighbor 8m or More) During the Wet Season.



Solitary Feeding (Nearest Neighbor 8m or More) During the Dry Season.

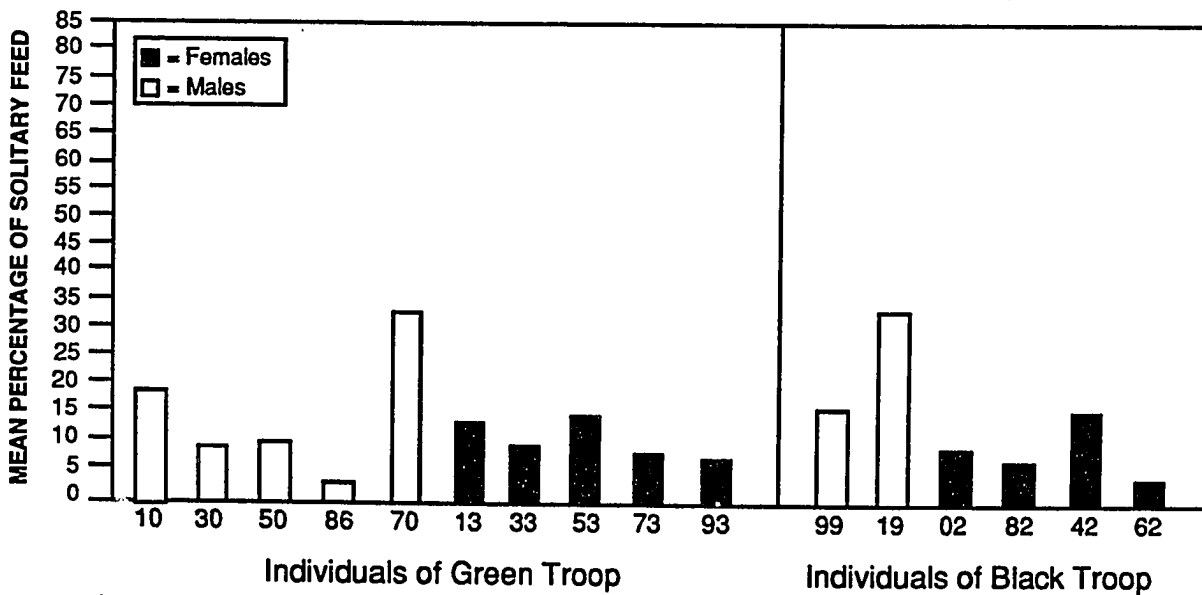


Figure 4.1. Mean Percentage of Solitary Feeding During the Wet and Dry Season

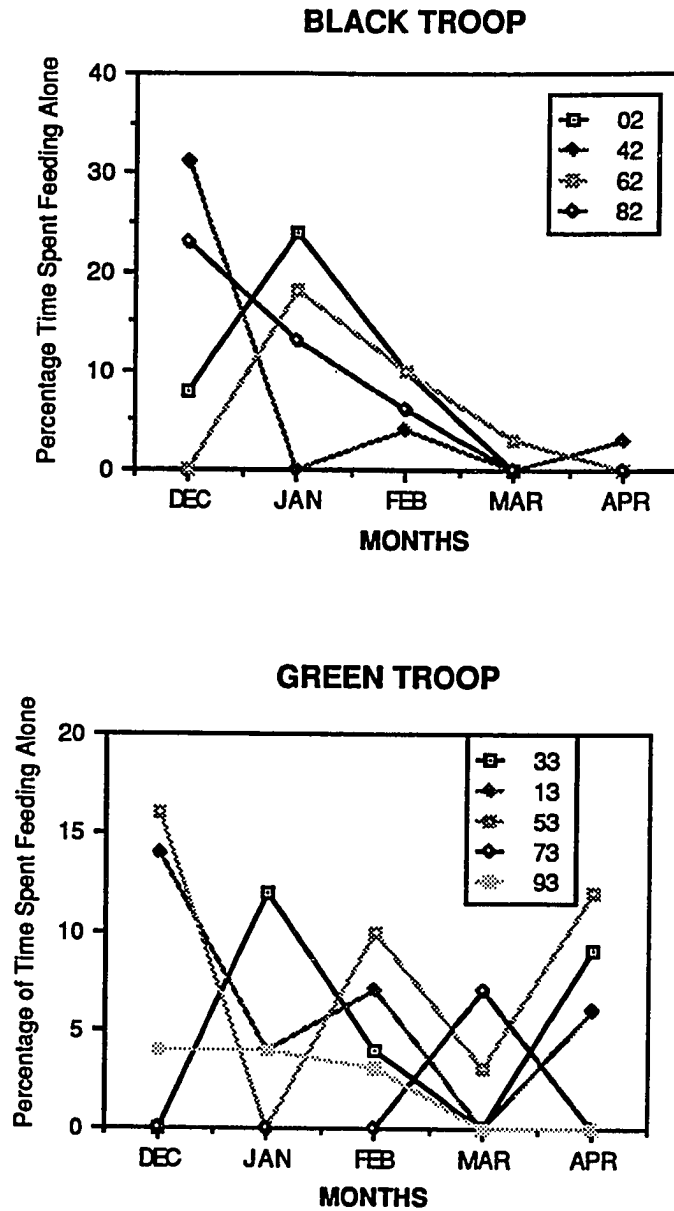


Figure 4.2 Time Spent Feeding Alone by Females of Black and Green Troop.

During the dry season there were no clear patterns among females in solitary feeding, although nearly all individuals reduced time spent feeding alone relative to the wet season. Males also reduced solitary feeding in the dry season, but in both troops the lowest-ranking males (Green troop: male 70; Black troop: male 19) still spent the greatest amount of time feeding alone.

Nearest Neighbor Dyads

The patterning of nearest neighbors might vary depending on reproductive state or kinship. Table 4.1 and 4.2 presents the mean percentage of time pairs of individuals were each other's nearest neighbors when both were feeding. During the wet season lactating females were rarely nearest neighbors during feeding bouts (Black Troop: 82 and 42, $p < 0.05$; Green Troop: 13 and 53, $p < 0.05$). However, closely related individuals (mother-daughter, mother-son) spent a greater percentage of time feeding near one another than near anyone else (Green Troop: 13 and 93, 53 and 73, 33 and 86, $p < 0.05$). In Black troop this also held true for the top-ranking female and her daughter (02 and 82, $p < 0.05$) but female 62, the daughter of female 42, spent similar amounts of time near the other two females.

Table 4.1. Mean percentage nearest neighbors while both feed during the wet and dry season in Green troop.

INDIVIDUALS	WET SEASON	DRY SEASON
02 & 42	3	2.2
02 & 62	9.4	5
02 & 82	19.4	1.2
02 & 99	6.8	2.8
02 & 19	8.4	3.8
82 & 42	1.4	8
82 & 62	9.8	11.2
82 & 99	4	8.4
82 & 19	7.2	4
42 & 62	10	13.2
42 & 99	5.6	8.8
42 & 19	2.8	5
62 & 99	7.8	10.6
62 & 19	4	9.2
99 & 62	1	0
99 & 19	5.6	3.8

Table 4.2 Mean percentage nearest neighbors while both feed during the wet and dry season in Green troop.

INDIVIDUALS	WET SEASON	DRY SEASON	INDIVIDUALS	WET SEASON	DRY SEASON
13 & 33	3	1.8	53 & 86	3	3
13 & 53	.83	2.2	73 & 93	3.8	4
13 & 73	4.8	5	73 & 10	.33	3
13 & 93	8.2	2.2	73 & 30	0	4
13 & 10	.60	2.2	73 & 50	2	2
13 & 30	1.6	.33	73 & 70	0	-
13 & 50	.60	0	73 & 86	4	6
13 & 70*	.60	-	93 & 10	.33	3
13 & 86	4.8	1.8	93 & 30	.60	3
33 & 53	3	2	93 & 70	0	-
33 & 73	2.6	2.4	93 & 50	1	2
33 & 93	1	3	93 & 86	1.60	3
33 & 10	3.6	3.6	10 & 30	1.2	2.8
33 & 30	1	.33	10 & 70	1	-
33 & 50	1.4	1.4	10 & 50	6	3.6
33 & 70	1	-	10 & 86	2	2
33 & 86	7.8	2.2	30 & 70	.40	-
53 & 73	4	2.4	30 & 50	0	1.2
53 & 93	1.6	4.2	30 & 86	2.4	1
53 & 10	2	0	50 & 70	.83	-
53 & 30	2	1.8	50 & 86	.33	1.4
53 & 50	3	3.4	86 & 50	0	0
53 & 70	1.6	-	86 & 70	1	-

*This individual transferred to Blue Troop during the dry season.

During the dry season when all females were pregnant, neither relatedness nor reproductive state helped explain nearest neighbors during feeding bouts. In fact, for all females except the lowest-ranking, the most common nearest neighbor was an individual who could be displaced from a feeding site (i.e. a male, or a lower ranking female), and for all dyads but one, (Black Troop: 42 and 62) the nearest neighbor was not closely related (i.e. not mother-offspring) (Black Troop: 02 and 62, 82 and 62; Green Troop: 13 and 73, 33 and 10, 53 and 93, 73 and 86).

Gender Effects

Tables 4.3 and 4.4 show mean percentages during which each individual had a male or a female as the nearest neighbor while both fed. Because there were only two males in Black Troop, the statistical analyses between males are confined to Green Troop. For females, no consistent pattern was discerned during the wet season, although most females had other females rather than males as their most frequent nearest neighbor. Among females, certain individuals did have lower percentages of female as their nearest neighbors. In both troops this was a lower-ranking, lactating female (42 of black troop, $p < .05$; 53 of Green troop, $p < .05$ for all but 53 and 33). Of the males, the natal male 86 had the highest percentage of female nearest neighbors. This is primarily due to his close association with his mother, 33 (see Table 4.2).

Table 4.3. Mean percentage of time spent as nearest neighbors for males and individual females when both were feeding in Green troop.

Percentage Time Nearest Neighbor Was Male

Individual	Female's Rank	Wet	Dry
13	1	1.64	.87
33	2	2.96	1.88
53	3	2.32	2.05
73	4	1.27	3.75
93	5	.71	2.75
10	6	2.55	2.80
30	7	1.00	1.66
50	8	1.79	2.06
86	9	1.43	1.47
70	10	.81	-

Percentage Time Nearest Neighbor Was Female

Individual	Female's Rank	Wet	Dry
13	1	4.21	2.80
33	2	2.40	2.30
53	3	2.36	2.70
73	4	3.80	3.45
93	5	3.65	3.35
10	6	1.37	2.36
30	7	1.04	1.51
50	8	1.60	1.76
86	9	4.24	3.20
70	10	.64	-

Table 4.4. Mean Percentage of Time Spent as Nearest Neighbors for Males, Females and Individual Females of Black Troop When Both were Feeding.

Percentage Time Nearest Neighbor Was Male

Individual	Female's Rank	Wet	Dry
02	1	7.60	3.30
82	2	5.60	6.20
42	3	4.20	6.90
62	4	5.90	9.90
99	5	5.60	3.80
19	6	5.60	3.80

Percentage Time Nearest Neighbor Was Female

Individual	Female's Rank	Wet	Dry
02	1	10.60	2.80
82	2	10.20	6.80
42	3	4.73	7.80
62	4	9.73	9.80
99	5	6.05	7.65
19	6	5.60	5.50

During the dry season lower-ranking females had males more often as their nearest neighbor than higher-ranking females ($p < .05$). Among males, the peripheral behavior of male 70 again stands out by his low percentage of both male and female nearest neighbors.

Distances Between Nearest Neighbor

Fig. 4.3 shows the mean percentage of nearest neighbors during feeding by distance, gender and troop. This measure can be used to represent how dispersed individuals were when feeding during the wet versus the dry season. Compared to the dry season, individuals tended to be more dispersed when feeding in the wet season. Percentages of close nearest neighbors (0-3 m) were markedly less during the wet versus dry seasons, whereas percentages of distant nearest neighbors (07->9 m) were higher during the wet season. Breaking down these measures by gender, and comparing wet and dry seasons, it can be seen that males, but not females significantly increased the percentage of close nearest neighbors in the dry season (i.e. they were not feeding closer to others). The percentage of close nearest neighbors during feeding for females remained the same, regardless of the season. Both males and females reduced distant nearest neighbors during the dry season.

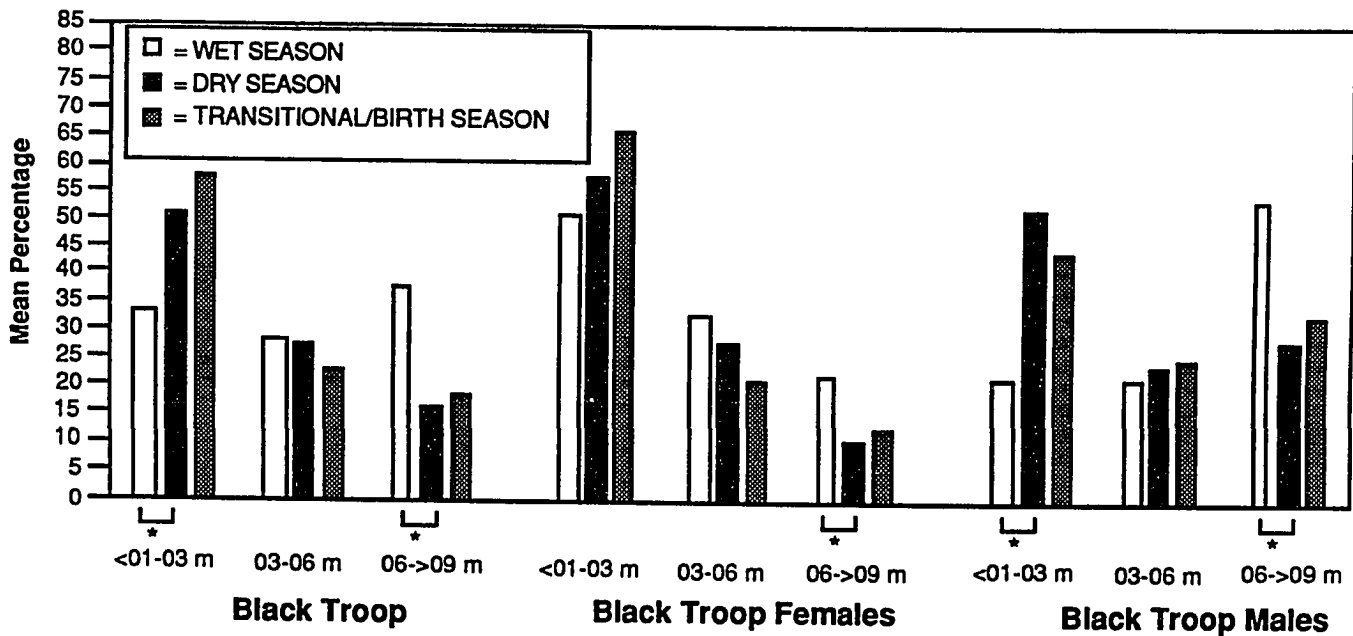
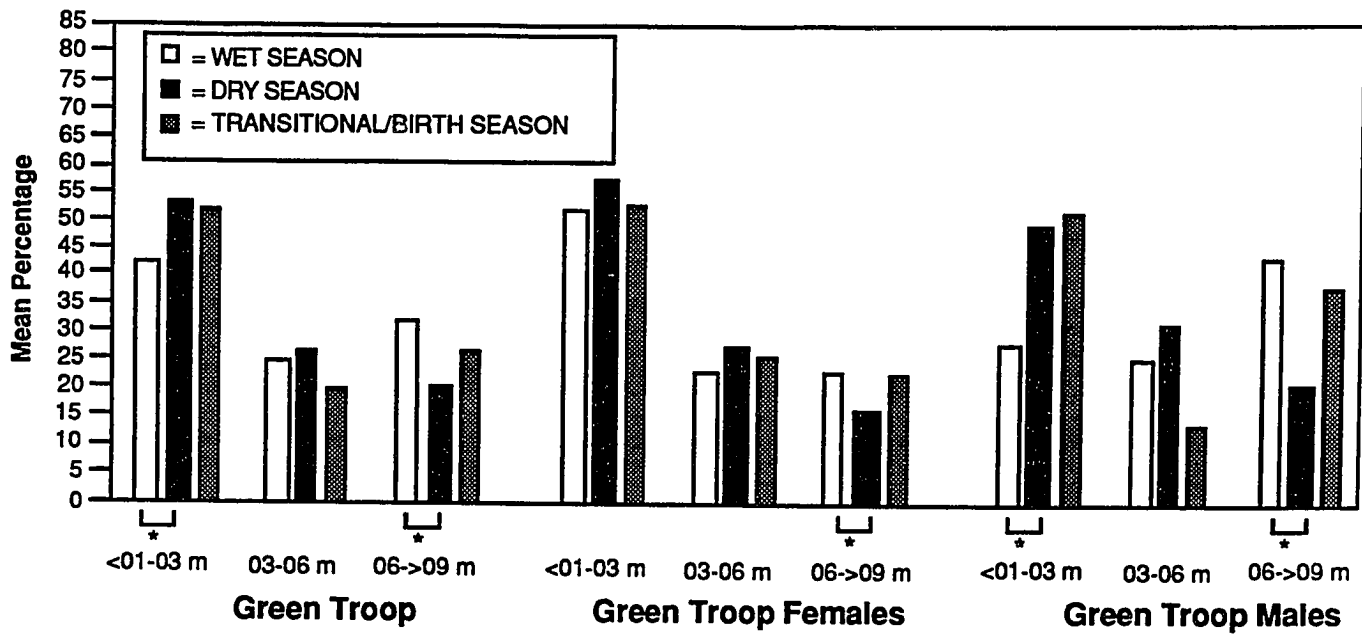
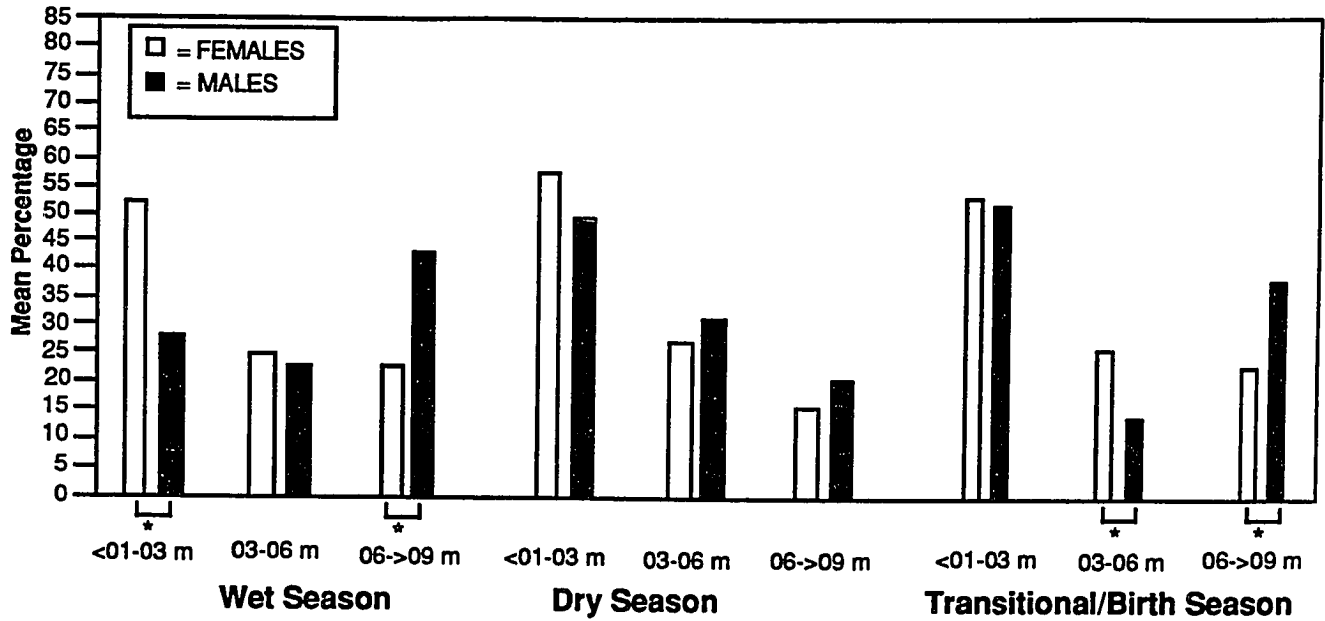


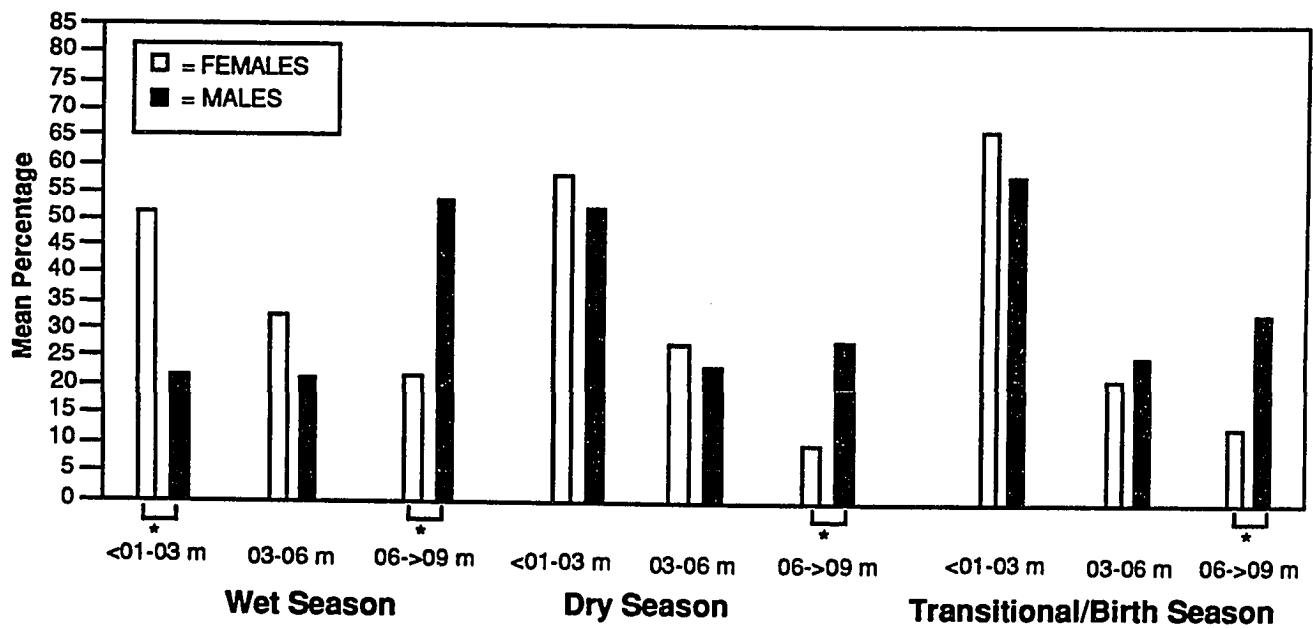
Figure 4.3. Mean Percentage Distances of Nearest Neighbors.

Figure 4.3 also compares these measures during the transitional birth season. At this time the trend for more dispersed feeding begins, with higher percentages of distant nearest neighbors than in the dry season. More importantly, it can be seen that females have higher percentages of close or intermediate nearest neighbors whereas males have more dispersed nearest neighbors at this time.

Figure 4.4 compares males and females for nearest neighbor distances. In both troops females had higher percentages of close (<01-03 m) neighbors while feeding during the wet season than did males. Males had higher percentages of distant (06->9 m) neighbors during feeding bouts in the wet season. In the dry season there were no meaningful gender differences for close neighbors. Males did tend to have more distant neighbors, but this was only significant for Black troop.

GREEN TROOP

* p < .05

Black Troop

* p < .05

Figure 4.4. Mean Percentage Distances of Nearest Neighbors by Gender.

LOCOMOTION

Types of Movement, and Movement Ratios

Types of movement could vary in important ways among individuals. Walking can be seen as a less energetic form of movement, whereas climbing, running and leaping are probably more costly. In Table 4.5 the mean percentage of time spent in active movement (climb, run, leap, hop, jump) and in walking is shown, along with a movement ratio. The movement ratio is simply the total time spent in active movement ÷ total time spent walking. Ratios greater than 1 indicate more active movement relative to walking. There were rank effects for all seasons among both males and females. Most lower-ranking males spent more time in active movement than higher-ranking individuals ($p < .05$). The only exception was male 70, the most peripheral individual, who showed the lowest percentage of active movement of all troop individuals, male and female. Movement ratios also reflect a high rank advantage for the wet season, but not so clearly in the dry season.

Table 4.5. Mean percentage of time spent in active movement (climb, leap, hop, run), walking, and movement ratio.

BLACK TROOP

Individual	Rank	ACTIVE		WALK		*RATIO	
		Wet	Dry	Wet	Dry	Wet	Dry
02	1	27%	27%	73%	73%	.42	.43
82	2	22%	40%	78%	50%	.30	.50
42	3	35%	31%	65%	69%	.66	.56
62	4	32%	34%	68%	66%	.57	.63
99	5	23%	17%	77%	83%	.54	.23
19	6	33%	27%	67%	73%	.29	.39

GREEN TROOP

Individual	Rank	ACTIVE		WALK		*RATIO	
		Wet	Dry	Wet	Dry	Wet	Dry
13	1	22%	15%	78%	85%	.30	.23
33	2	36%	24%	64%	76%	.46	.32
53	3	48%	37%	52%	63%	.74	.63
73	4	47%	41%	53%	59%	.93	.85
93	5	47%	39%	53%	61%	.62	.75
10	6	33%	34%	67%	66%	.52	.52
30	7	34%	40%	66%	60%	.62	.75
50	8	43%	43%	57%	57%	.76	.54
86	9	42%	45%	58%	55%	.77	.94
70**	10	18%	25%	82%	75%	.24	.36

*Ratio of 1 = equal time spent in active movement and walking. The higher the ratio, the more active movement utilized.

**This male transferred to Blue Troop during the dry season.

Among females, the two top-ranking females in each troop used less active forms of movement than lower-ranking females ($p < .05$). Again movement ratios also reflect this. Lower ranking females all tended to use similar percentages of active movement.

NONFOOD RESOURCES

Water

The mean percentage of time spent drinking at tree hollows is represented in Fig 4.5. Social rank effects were clear among males and females, with higher-ranking individuals spending a markedly greater percentage of time drinking at these sites than lower-ranking individuals of the same sex ($p < .05$). Comparing males and females, the top-ranking females (Green Troop: 13, 33; Black Troop: 02, 82) spent equal or greater time drinking at these sites than males (Green: 10 & 73, 10 & 53, 30 & 73, 30 & 93, 30 & 53; Black: 99 & 63, $p < .05$). Top-ranking males (Green Troop: 10, 30; Black Troop: 99) were able to spend similar or greater amounts of time drinking at these sites than some low ranking females, however.

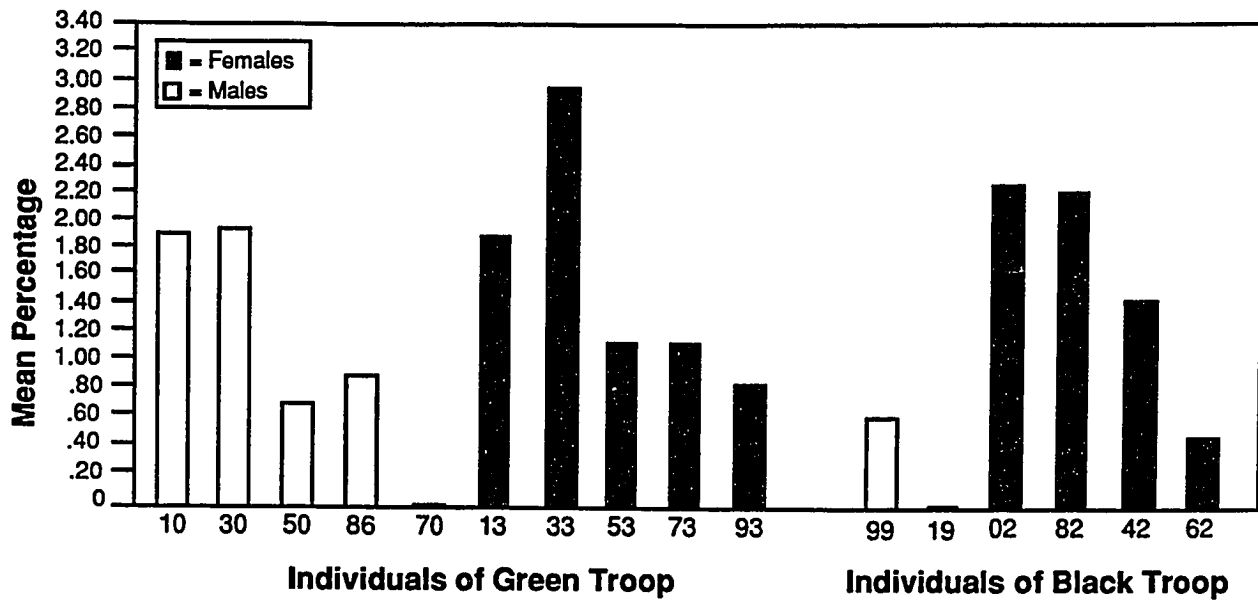


Figure 4.5. Mean Percentage of Time Spent Drinking at Tree Hollows during the Wet Season.

Spatial Agonism

Agonistic displacements occurred relative to access to resting and sunning areas and are referred to as "spatial" agonism. In Table 4.6 the percentage of total spatial agonism which occurred between females, males and females and between males is shown. In the wet season more spatial agonism occurred between males and females, but during the dry season the highest spatial agonism was between female dyads. Male-male spatial agonism was consistently lower than all other dyads regardless of season.

Table 4.6. Comparison of the percentage of total spatial agonism for female-female, female-male and male-male dyads in Black and Green troop.

BLACK TROOP

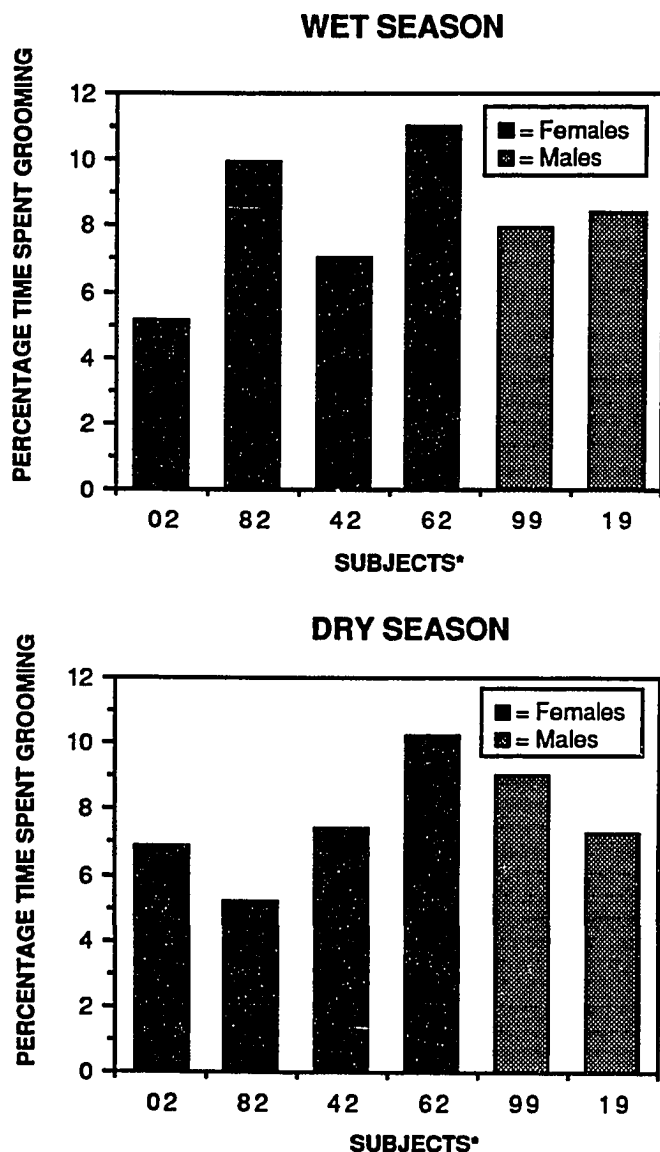
DYADS	WET	DRY
Female-Female Female-Male Male-Male	46% 52% 2%	87% 12% 1%
Female-Female vs. Female-Male	$p < .05$	$p < .001$
Female-Female vs. Male-Male	$p < .05$	$p < .05$
Female-Male vs. Male-Male	$p < .05$	$p < .05$

GREEN TROOP

DYADS	WET	DRY
Female-Female Female-Male Male-Male	33% 46% 21%	53% 35% 12%
Female-Female vs. Female-Male	$p < .05$	$p < .05$
Female-Female vs. Male-Male	$p < .05$	$p < .05$
Female-Male vs. Male-Male	$p < .05$	$p < .05$

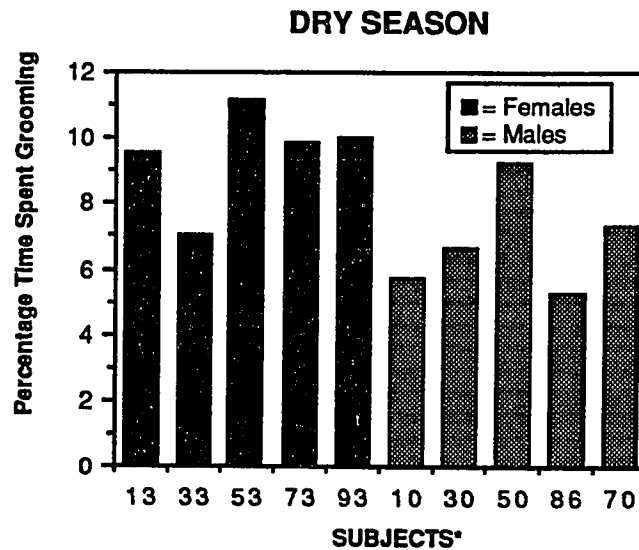
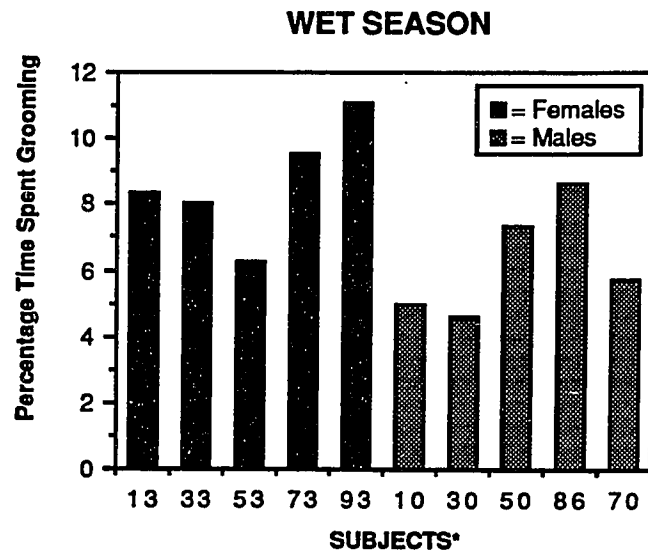
Grooming

Fig. 4.6 and 4.7 shows the percentage of time spent either autogrooming or mutual grooming. Individuals are arranged in descending rank order. For both troops and both seasons, and within the same gender the trend was for lower ranking individuals to spend more time in grooming activities.



*Subjects are arranged by rank in descending order.

Figure 4.6. Percentage of Time Spent Grooming by Members of Black Troop.



*Subjects are arranged by rank in descending order.

Figure 4.7. Percentage of Time Spent Grooming by Members of Green Troop.

AGONISM OVER FOOD RESOURCES

Birth Day-Follows

The mean percentages of wins associated with agonistic displacements in a feeding and foraging context during the continuous birth season day-follows are illustrated in Figure. 4.8. In general, females had markedly higher mean percentages of wins during feeding than did males ($p < .05$), although this was true only for the two top-ranking females in Black Troop (02 and 82). A similar pattern for most females occurred for wins in a foraging context.

High ranking females (13 of Green Troop, 02 and her daughter 82 of Black Troop) were responsible for a disproportionate percentage of wins in a feeding context, as well as during foraging, although the latter was less dramatic. Central males in both troops (10 of Green Troop and 99 of Black Troop) had a higher mean percentage of wins during feeding than the other male(s), but not during foraging.

Figure 4.9 shows the percentage of losses for birth season day follows. Most females had a low percentage of losses compared to males. However, females 53 of Green Troop and 42 and her daughter 62 of Black Troop actually had higher percentages of feeding losses than males of their respective troops. The lowest-ranking female of Black troop (62) had very high losses during foraging. Males had higher percentages of losses in foraging contexts than all females except the lowest-ranking female in Black troop (62).

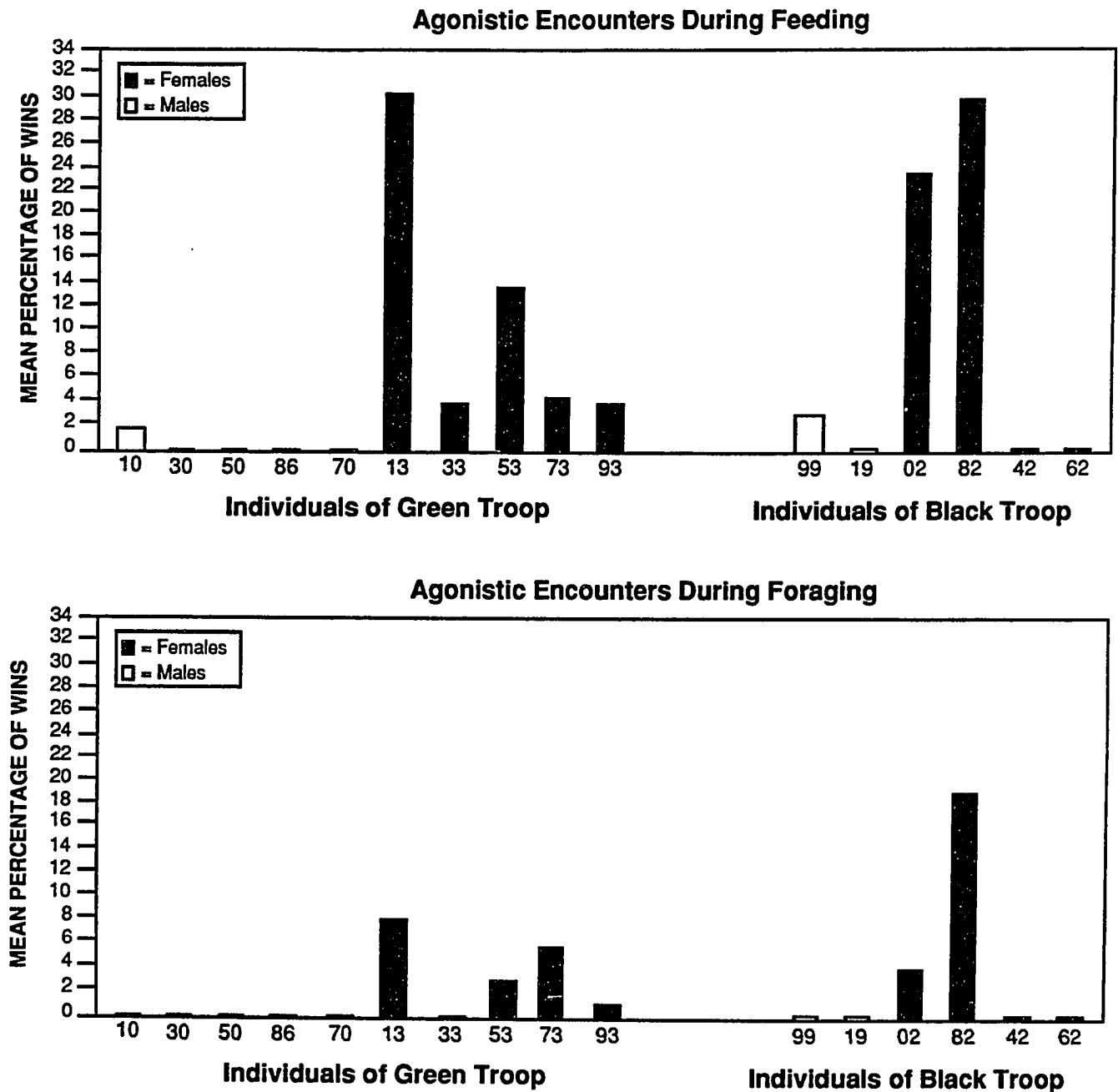


Figure 4.8 Mean Percentages of Wins for Agonistic Encounters by Individuals During Birth Season Day Follows.

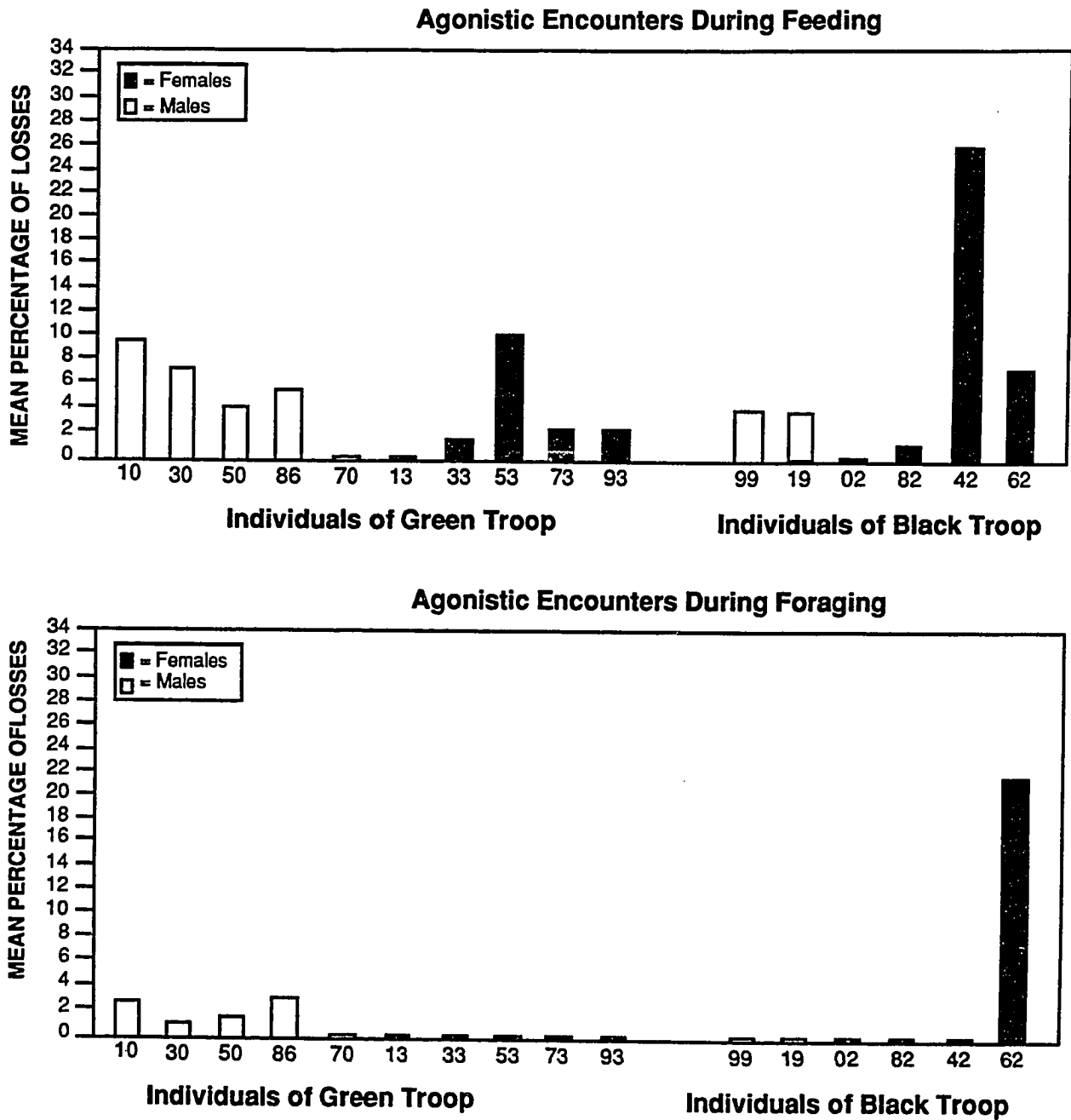


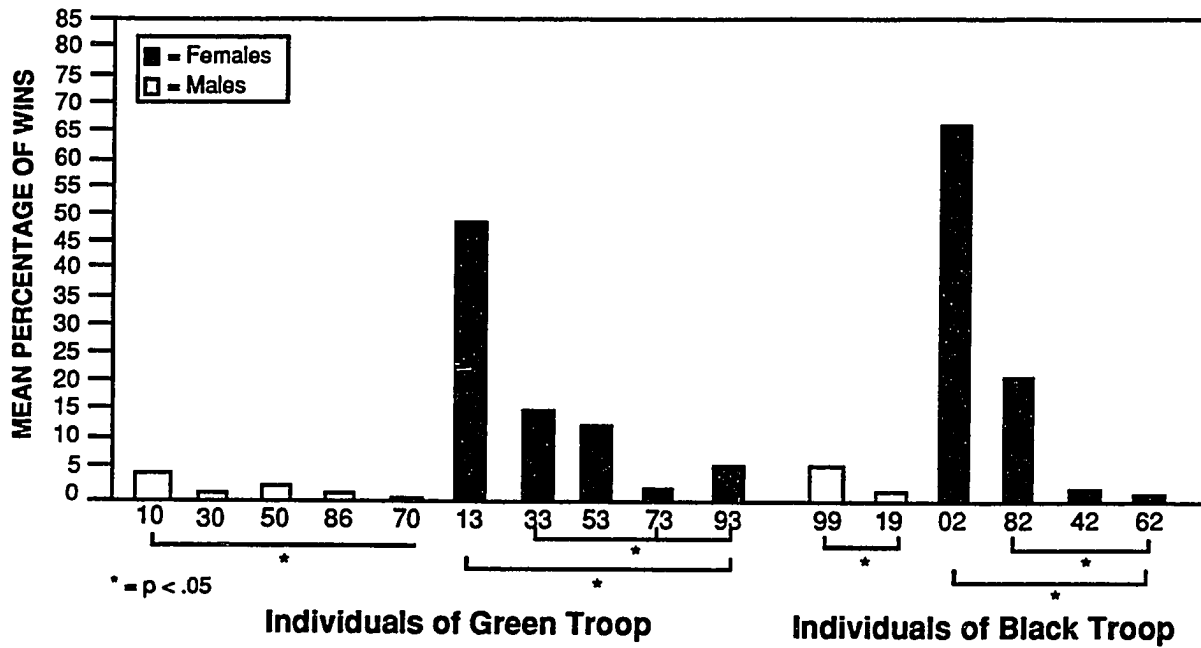
Figure 4.9 Mean Percentages of Losses by Individuals During Agonistic Encounters During Birth Season Day Follows.

Wet and Dry Season

Fig. 4.10 illustrates the mean percentage of wins during agonistic encounters over food during the wet and dry season. As during the birth season, high-ranking females had a greater percentage of wins than all other individuals, male and female. For both wet and dry season, central males in these troops won more of these bouts than other, lower ranking males ($p < .05$). The same pattern occurred for females during the wet season, with higher ranking females winning more of these bouts. During the dry season, this pattern still held although in Green troop the third-ranking female (53), had more wins than the second-ranking female (33), although not markedly so.

Fig. 4.11 shows the percentage of losses during such encounters. Among males, during the wet season the Central male (10) and male 86 of Green Troop had more losses than other males, while in Black Troop the central male (99) had fewer losses. During the dry season, most males in Green Troop showed similar percentages of losses, while in Black Troop the central male again had fewer losses.

Agonistic Encounters During Feeding: Wet Season



Agonistic Encounters During Feeding: Dry Season

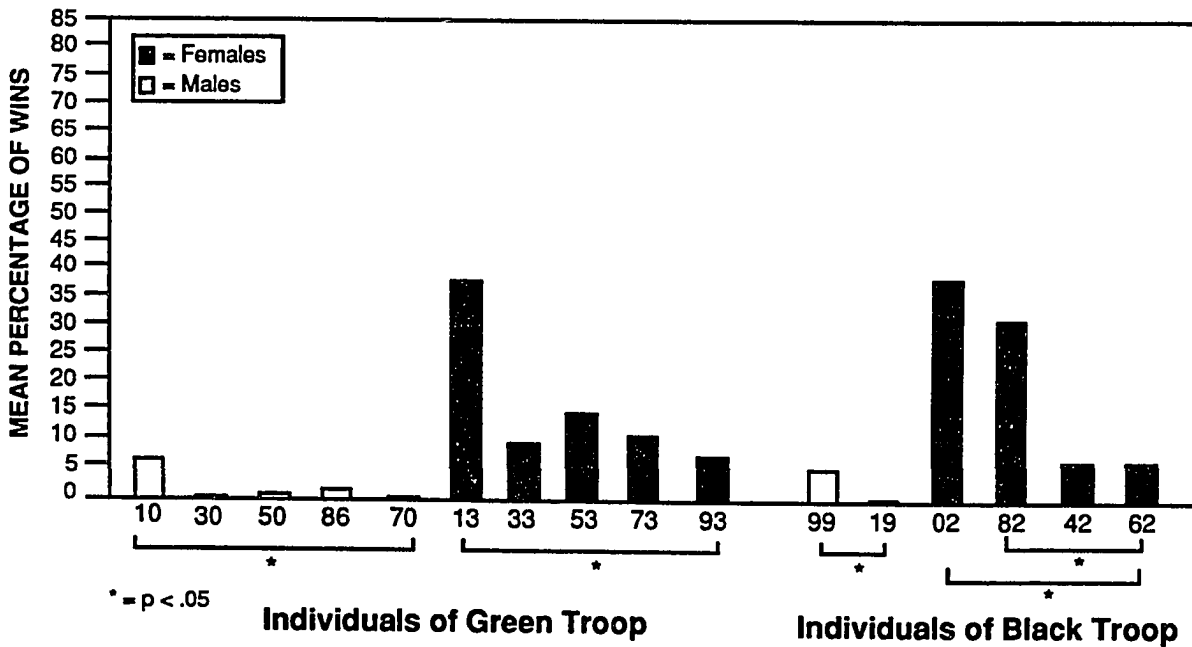


Figure 4.10. Mean Percentages of Wins During Agonistic Encounters Over Food During the Wet and Dry Seasons.

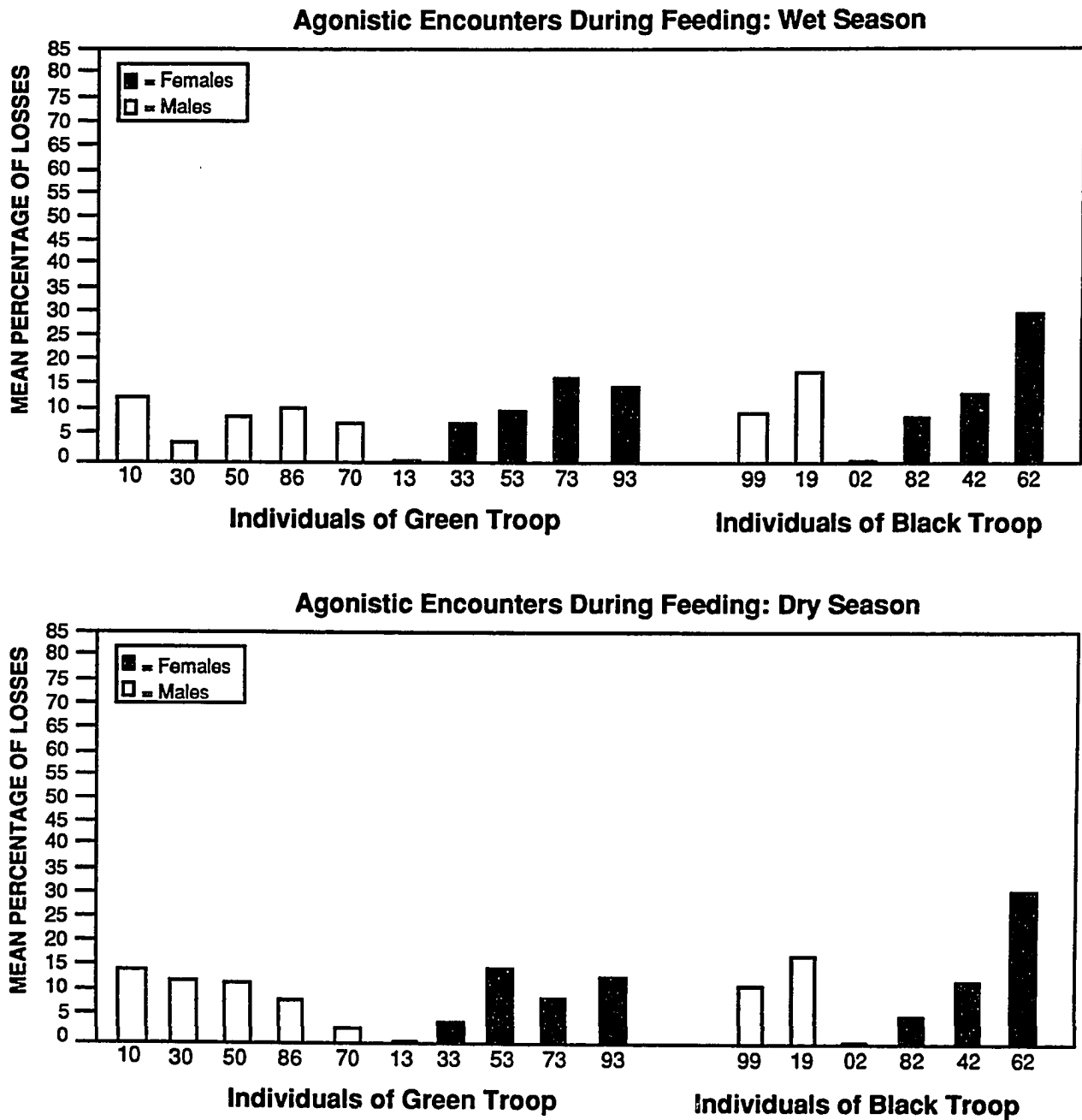


Figure 4.11. Mean Percentages of Losses during Agonistic Encounters During the Wet and Dry Seasons.

Among females, during both seasons lower-ranking females suffered greater losses than higher-ranking females. Some lower-ranking females had losses equal to or greater than some males (Green troop Wet Season: 73, 53, 93, Dry Season: 73, 53, 93; Black troop Wet and Dry Season: 42, 62).

Types of Displacement Relative to Social Rank

Percentage of feeding displacements where the individual was the winner were separated into two types. Complete displacement (CD) refers to feeding displacements where the displacing individuals also fed from the same patch they attained. Incomplete displacement (ID) was when the individual displacing another did not feed from the same patch. These results are shown in Tables 4.7 and 4.8. For both troops, higher rank was associated with a higher percentage of wins for displacements of both types.

Table 4.7. Mean percentage of complete and incomplete displacement during feeding bouts in Black troop by season.

Winner	Rank	WET SEASON		DRY SEASON	
		Complete *Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
02	1	40.90	23.10	36.80	17.80
82	2	15.60	6.80	14.20	3.20
42	3	3.40	.70	8.90	1.60
62	4	0	.70	2.40	3.80
99	5	5.40	2.70	4.80	5.60
19	6	0	.70	.96	0

*Displacement Complete refers to spatial displacement of one individual by another during feeding where the animal displacing also feeds at the attained feeding site. In incomplete displacement an individual is displaced from a feeding site but the displacing individual does not feed at the site.

Table 4.8. Mean percentage of complete and incomplete displacement during feeding bouts in Green troop by season.

WET SEASON				DRY SEASON	
Winner	Rank	Complete Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
13	1	27.50	21.90	27.60	11.00
33	2	12.70	7.70	5.00	6.40
53	3	14.20	6.90	10.20	5.10
73	4	.20	.70	8.80	5.50
93	5	2.40	0	6.90	1.80
10	6	3.20	.70	3.70	2.30
30	7	.70	.50	1.80	2.30
50	8	.90	.40	1.80	.50
86	9	1.20	.20	6.90	1.80
**70	10	.28	.50	-	-

*Displacement Complete refers to spatial displacement of one individual by another during feeding where the animal displacing also feeds at the attained feeding site. In incomplete displacement an individual is displaced from a feeding bout but the displacing individual does not feed at the site.

**This male migrated from Green Troop during the dry season.

Comparing the wet and dry seasons, in both troops the percentage of CDs remained similar or decreased for top-ranking females (Green Troop: females 13, Black Troop, female 02) but increased among lower-ranking females (Green Troop: females 73, 93; Black Troop: 62, 42).

Among males CDs were similar during the wet and dry season among high-ranking individuals (Green troop: 10; Black troop: 99), but were higher in the wet season for lower-ranking males than during the dry season (Green Troop: 30, 50, 86; Black troop: 19).

Comparing incomplete displacements, in both troops higher-ranking individuals (Green Troop: females 13, 33, 53; Black Troop: females 02, 82) decreased their percentage of IDs from wet to dry season, whereas lower-ranking females increased their percentage of IDs (Green Troop: females 73, 93; Black Troop: 42, 62). Among males, IDs tended to increase during the dry season.

Food- and NonFood-Related Agonism by Gender, Displacement Type and Season

In Table 4.9 and 4.10 agonistic dyads are presented by displacement type wherein the loser is either male or female. During the wet season most of the feeding agonism toward males was from females. Comparing wet and dry seasons indicates that lower-ranking females increased percentages of complete and incomplete displacements directed towards males during the dry season, whereas high-ranking females maintained or decreased agonism toward males. In general, most females maintained or decreased feeding agonism with other females during the dry season.

Table 4.9. Agonistic dyads during feeding by gender and displacement type in Green troop.

Wet Season

Dry Season

Percentage Loser Was Male

Winner	Winner's Rank	Complete Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
13	1	10.50	7.70	11.50	4.10
33	2	6.70	3.20	1.80	3.50
53	3	9.70	3.20	5.10	3.70
73	4	0.20	0.50	7.40	4.60
93	5	2.20	0	6.90	1.80
10	6	3.20	0.20	3.70	2.30
30	7	0.70	0.50	1.80	2.30
50	8	0.20	0.20	1.80	0.50
86	9	0.20	0	6.90	1.80
70*	10	.28	.50	0	-

Wet Season

Dry Season

Percentage Loser Was Female

Winner	Winner's Rank	Complete Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
13	1	17.00	14.20	16.10	6.90
33	2	6.00	4.50	3.20	0.90
53	3	3.50	2.70	5.10	1.40
73	4	0	0.20	1.40	0.90
93	5	0.20	0	0	0
10	6	0	0.50	0	0
30	7	0	0	0	0
50	8	0.70	0.20	0	0
86	9	1.00	0.20	0	0
70*	10	0	0	0	-

*This male transferred to Blue Troop During the Dry Season.

Table 4.10. Agonistic Dyads during Feeding by Gender and displacement type in Black Troop.

Wet Season				Dry Season	
Percentage Loser Was Male					
Winner	Winner's Rank	Complete Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
02	1	19.10	7.50	17.00	5.30
82	2	3.40	2.70	3.20	0.80
42	3	0.70	0	6.50	1.60
62	4	0	0	4.40	6.80
99	5	5.40	2.00	2.40	5.60
19	6	0	0	0.80	0

Wet Season				Dry Season	
Percentage Loser Was Female					
Winner	Winner's Rank	Complete Displacement	Incomplete Displacement	Complete Displacement	Incomplete Displacement
02	1	21.80	15.60	18.40	8.90
82	2	12.20	4.10	11.08	2.40
42	3	2.70	0.70	2.40	0
62	4	0	0.70	0	0
99	5	0	0.70	2.40	0
19	6	0	0.70	0	0

Total feeding agonism is broken down by gender in Figures 4.12 and 4.13. For both troops and for both seasons the same pattern is seen. Female-female feeding agonism is higher than any other dyad, although not markedly in Green Troop, and male-male feeding agonism makes up the least percentage of total agonism (significant for Green Troop at $p < .05$).

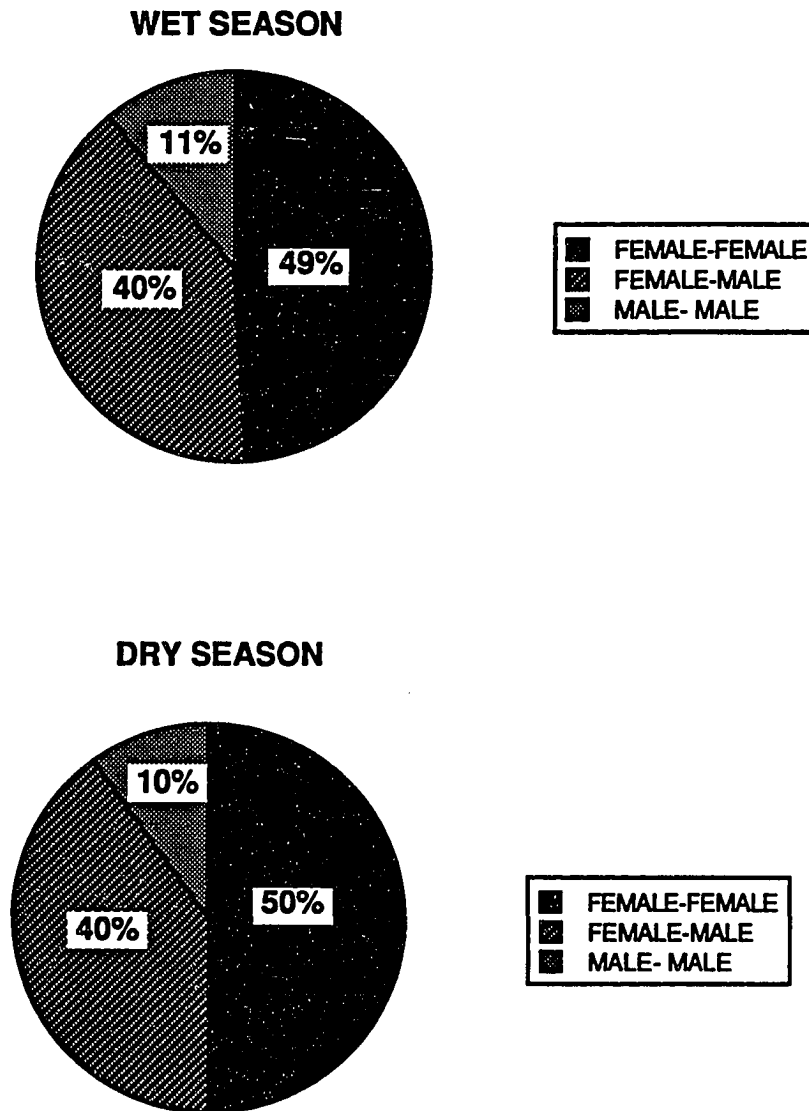


Figure 4.12 Total Feeding Agonism During the Wet and dry Season for Green Troop.

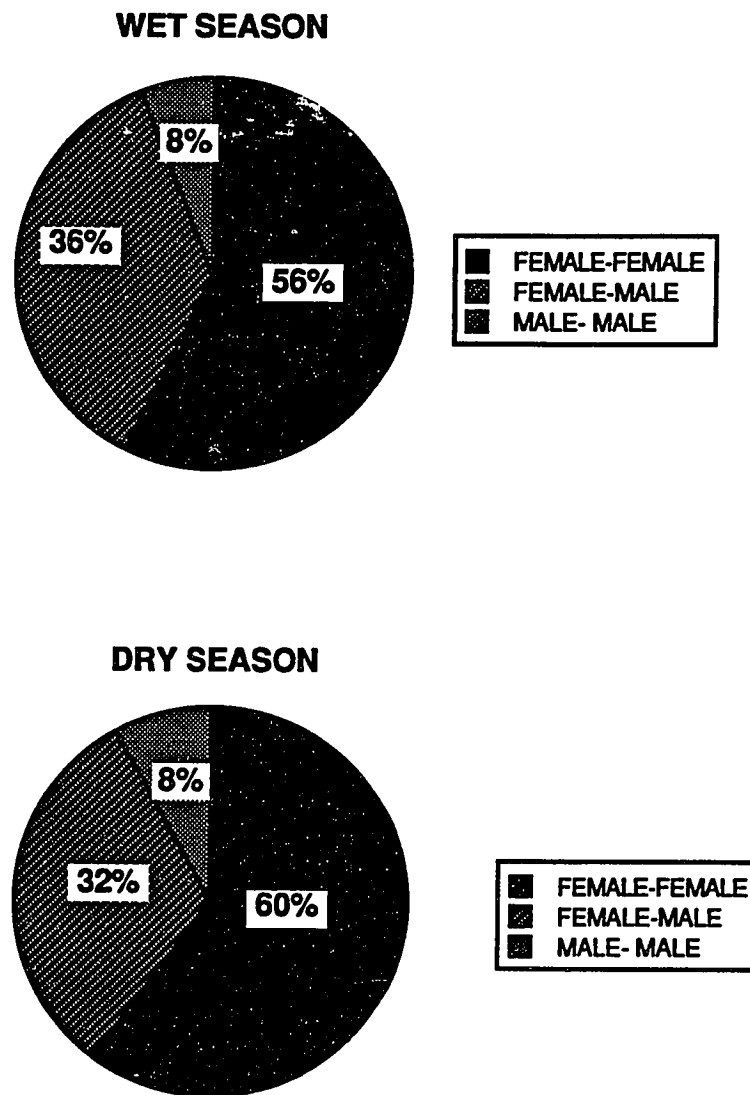


Figure 4.13 Total Feeding Agonism During the Wet and Dry Season for Black Troop.

In Table 4.11 all pairs are pooled and the relative mean percentage of agonism which occurred between females, males, or between females and males is shown. Agonism over food was greater during the wet season for female dyads, and greater in the dry season for female-male dyads, although this did not reach significance. Male dyads had a significantly higher mean percentage of feeding agonism during the dry season. Nonfeeding agonism did not vary significantly by season for any dyad.

Table 4.11. Mean percentage of relative feeding and non-feeding agonism for Female-Female, Female-Male and Male-Male Dyads.

FEEDING AGONISM

DYADS	WET	DRY	WET VERSUS DRY
Female-Female	7.21%	5.75%	N.S.
Female-Male	1.87%	2.60%	N.S.
Male-Male	1.24%	3.08%	$p < .05$

NON-FEEDING AGONISM

DYADS	WET	DRY	WET VERSUS DRY
Female-Female	3.79%	4.68%	N.S.
Female-Male	2.00%	2.32%	N.S.
Male-Male	.84%	.80%	N.S.

Pairwise Feeding Agonism

Tables 4.12 and 4.13 present the mean percentages of feeding agonism between pairs of individuals in Black and Green Troop. Several patterns emerge from this table. First, closely related pairs of individuals (e.g. mother-daughter or mother-son dyads) had relatively lower percentages of feeding agonism. In Black Troop, females 02 and 82 (mother-daughter) had lower agonism than all other female dyads involving female 02 ($p < .05$). Females 42

and 62 (mother-daughter), also had lower agonism ($p < .05$, except dry season 42 & 62 versus 82 & 62). Among females in Green Troop, 13 and 93 (mother-daughter) showed lower feeding agonism ($p < .05$ for wet season 13 and 93 versus 13 & 73; dry season 13 & 93 versus 13 & 53; 13 & 73; 13 & 30; 13 & 50). Female 33 and her son 86 also showed lower feeding agonism ($p < .05$) relative to all other pairs involving 33. Conversely, the highest feeding agonism occurred either between the highest-ranking female and the daughter of a lower-ranking female (Black Troop: 02 and 62, $p < .05$ for all pairs both seasons except 02 and male 19 during the wet season; Green Troop: 13 and 73, $p < .05$, wet season), or the highest-ranking female and a lower-ranking female (Green Troop: 13 and 53, $p < .05$, dry season).

While older adult females always won over males in agonistic feeding dyads, this was not absolute for younger females. Although the percentages are low, some males did decisively win over younger females during the wet season, but not during the dry season.

AGGRESSIVE AND NONAGGRESSIVE FEEDING AGONISM

Wet and Dry Seasons

Figure 4.14 illustrates the mean percentage of time each individual was involved in aggressive (those involving chasing, biting, and cuffing), agonistic encounters. Among most males, similar levels of aggressive agonism occurred during the wet and dry season. Among most of the females, aggressive encounters were higher during the wet season, although this did not reach significance for all females. Comparing the wet and dry seasons, it can be seen that high ranking females showed a greater reduction in aggressive feeding agonism in the dry season.

Table 4.12. Pairwise Feeding Agonism During the Wet and Dry Season in Green Troop.

INDIVIDUALS	WET SEASON	DRY SEASON	INDIVIDUALS	WET SEASON	DRY SEASON
13* & 33	6%	3%	73 & 50	0%	2%
13 & 53	6%	13%	73 & 70	1%	-
13 & 73	12%	4%	73 & 86	.01%	8%
13 & 93	5%	2%	93 & 73	.33%	0
13 & 10	5%	3%	93 & 10	.33%	3%
13 & 30	2%	4%	93 & 30	.16%	1%
13 & 50	2%	4%	93 & 70	2%	0
13 & 70**	.84%	-	93 & 50	1%	2%
13 & 86	6%	3%	93 & 86	0	.33%
33 & 53	3%	2%	10 & 73	0	0
33 & 73	3%	1%	10 & 93	.16%	0
33 & 93	2%	1%	10 & 30	1%	2%
33 & 10	4%	1%	10 & 70	1%	-
33 & 30	4%	2%	10 & 50	.16%	2%
33 & 50	1%	2%	10 & 86	2%	2%
33 & 70	.01%	-	30 & 73	0	0
33 & 86	0	0	30 & 93	0	0
53 & 73	3%	2%	30 & 70	1%	-
53 & 93	2%	3%	30 & 50	0	0
53 & 10	1%	2%	30 & 86	.50%	2%
53 & 30	3%	2%	50 & 73	.16%	0
53 & 50	.83%	1%	50 & 93	1%	0
53 & 70	.33%	-	50 & 86	.66%	1%
53 & 86	2%	1%	86 & 73	.50%	0
73 & 93	2%	0	86 & 93	1%	0
73 & 10	.33%	3%	86 & 50	0	0
73 & 30	0	2%			

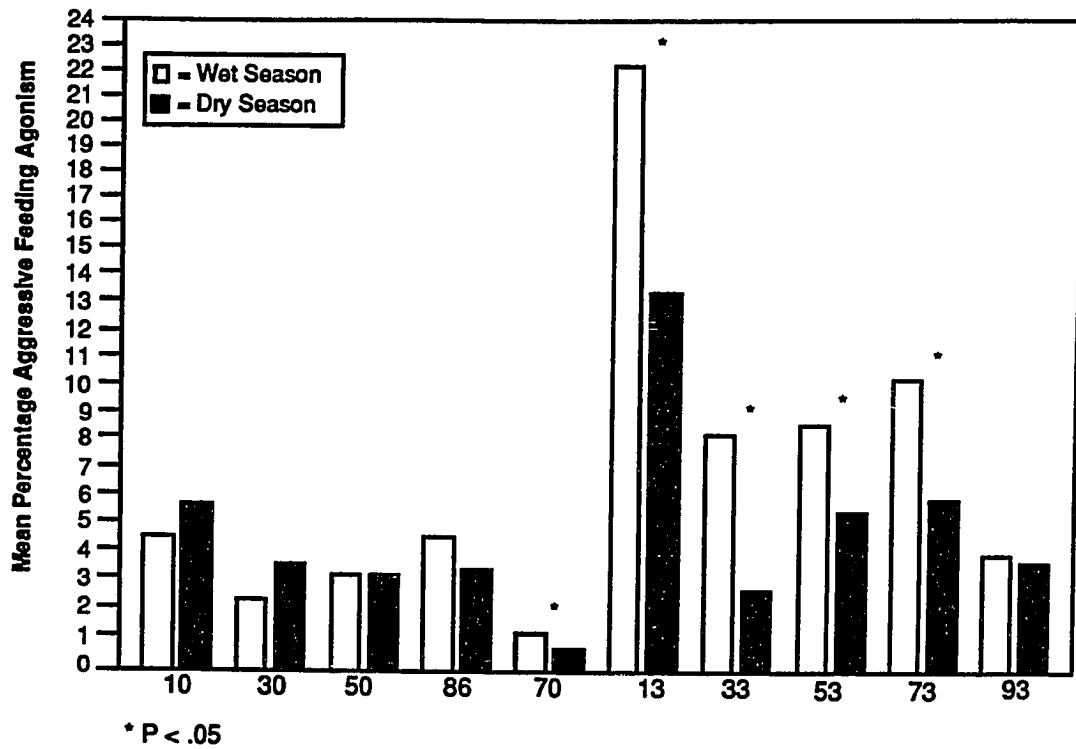
*The individual presented first is the winner

Table 4.13. Pairwise Feeding Agonism During the Wet and Dry Season in Black Troop.

INDIVIDUALS	WET SEASON	DRY SEASON
*02 & 42	10%	9%
02 & 62	19%	12%
02 & 82	7%	5%
02 & 99	9%	8%
02 & 19	21%	7%
82 & 42	7%	4%
82 & 62	9%	3%
82 & 99	3%	2%
82 & 19	1%	2%
42 & 62	1%	3%
42 & 99	1%	1%
42 & 19	0	4%
62 & 99	0	1%
62 & 19	0	3%
99 & 62	1%	0
19 & 62	1%	0
99 & 19	7%	10%

*The individual presented first is the winner.

GREEN TROOP



BLACK TROOP

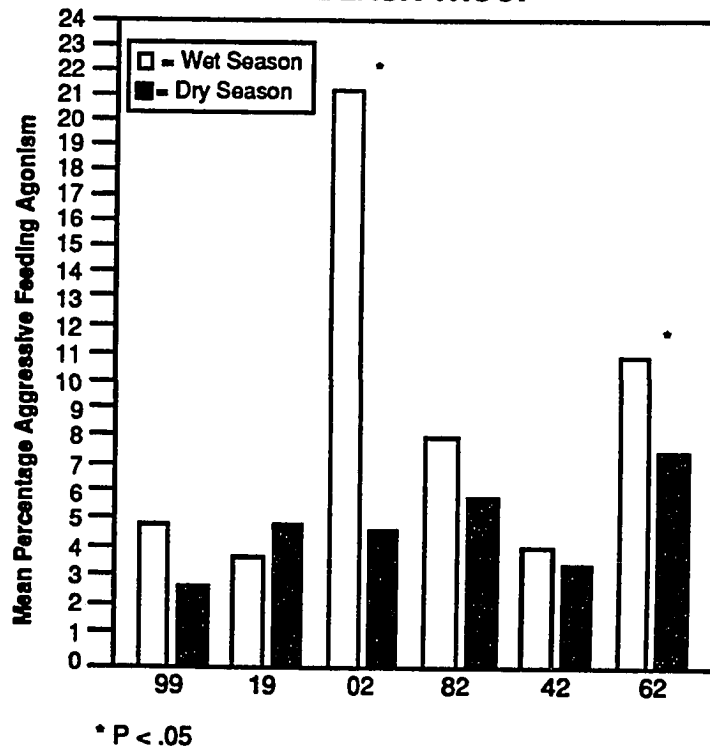


Figure 4.14. Mean Percentages of Time Involved in Aggressive Feeding Agonism During the Wet and Dry Seasons.

Fig 4.15 shows the percentage of nonaggressive feeding agonism (i.e. those involving only approaches and retreats) For most individuals, nonaggressive agonism was significantly greater during the dry season, compared to the wet season. Comparing the wet and dry seasons shows a greater increase in nonaggressive feeding agonism among low-ranking females.

Figure 4.16 and 4.17 compares the percentage of aggressive and nonaggressive feeding agonism, holding seasons constant. For most individuals, significantly more aggressive agonism occurred during the wet season. During the dry season the levels of aggressive and nonaggressive feeding agonism tended to be similar in Green Troop, but in Black troop more agonism was nonaggressive.

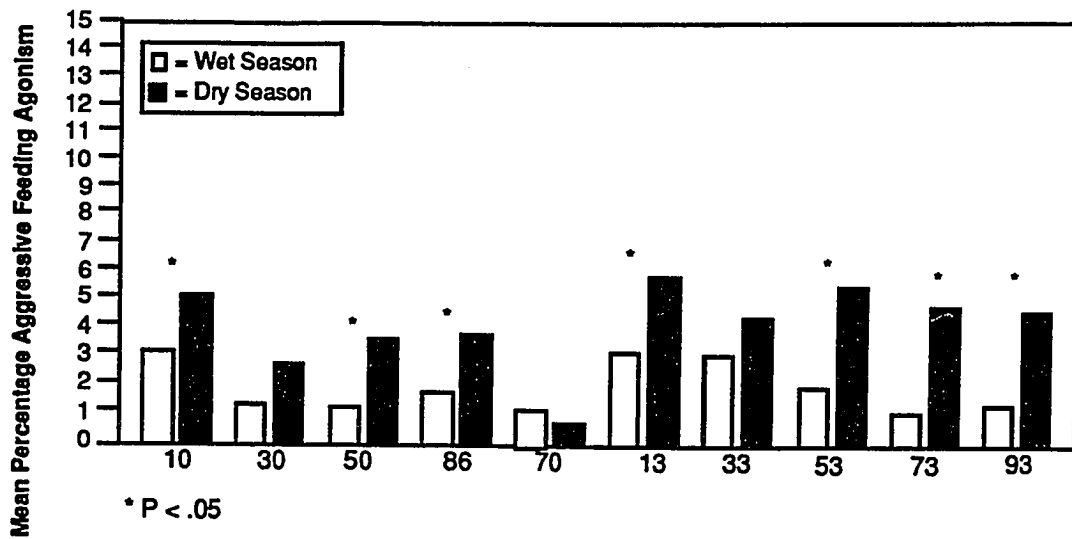
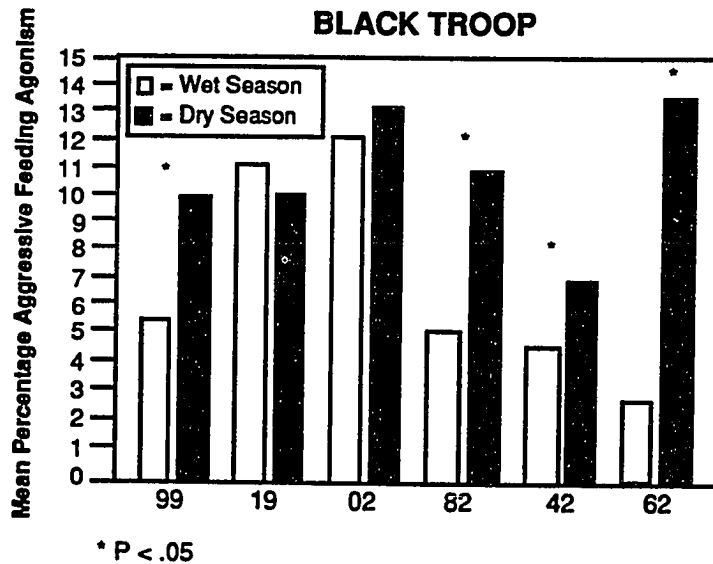
GREEN TROOP**BLACK TROOP**

Figure 4.15. Mean Percentages of Time Involved in Non-Aggressive Feeding Agonism During the Wet and Dry Seasons.

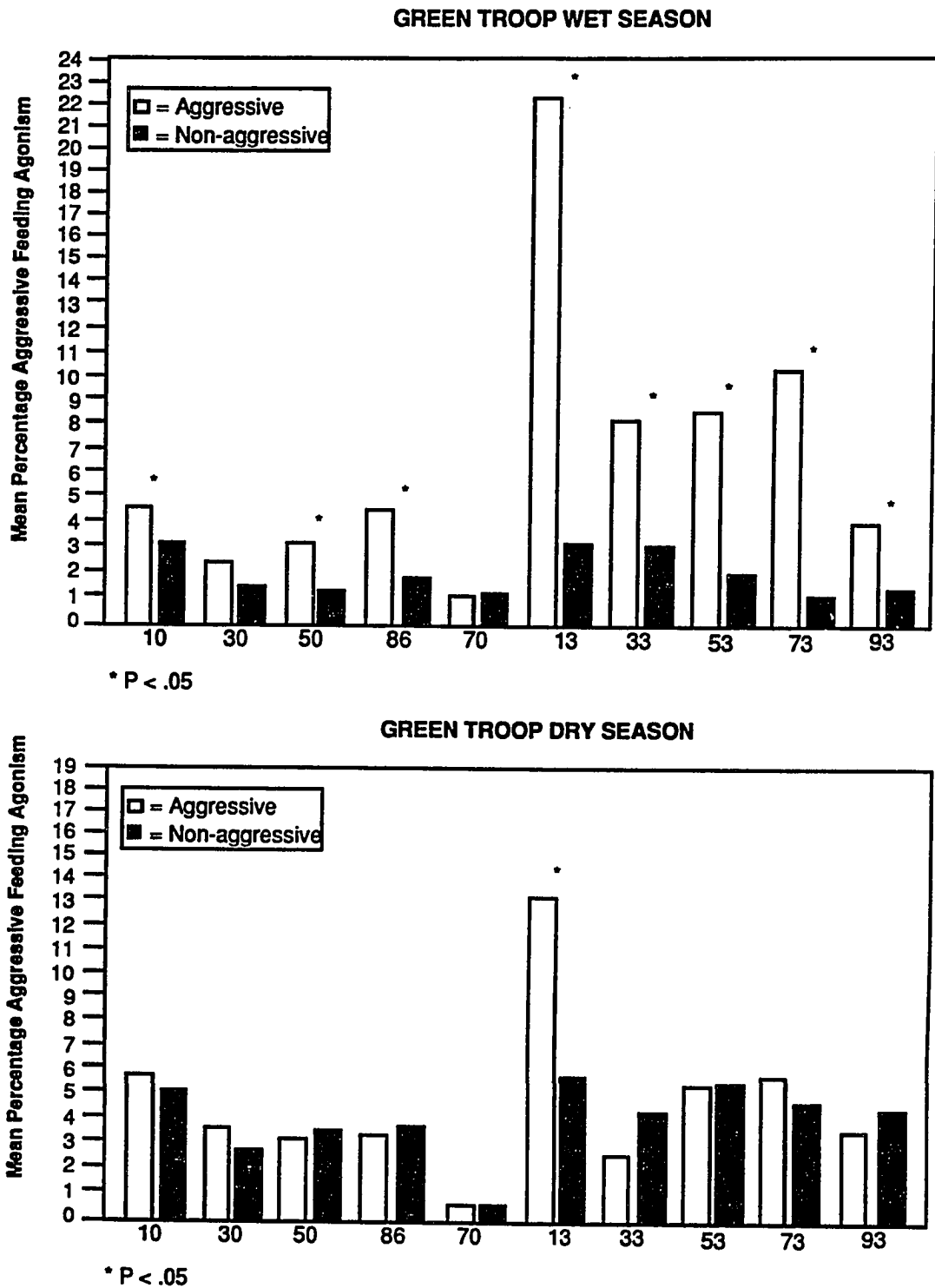


Figure 4.16. Mean Percentages of Time Involved in Aggressive Versus Non-aggressive Feeding Agonism During the Wet and Dry Seasons in Green Troop.

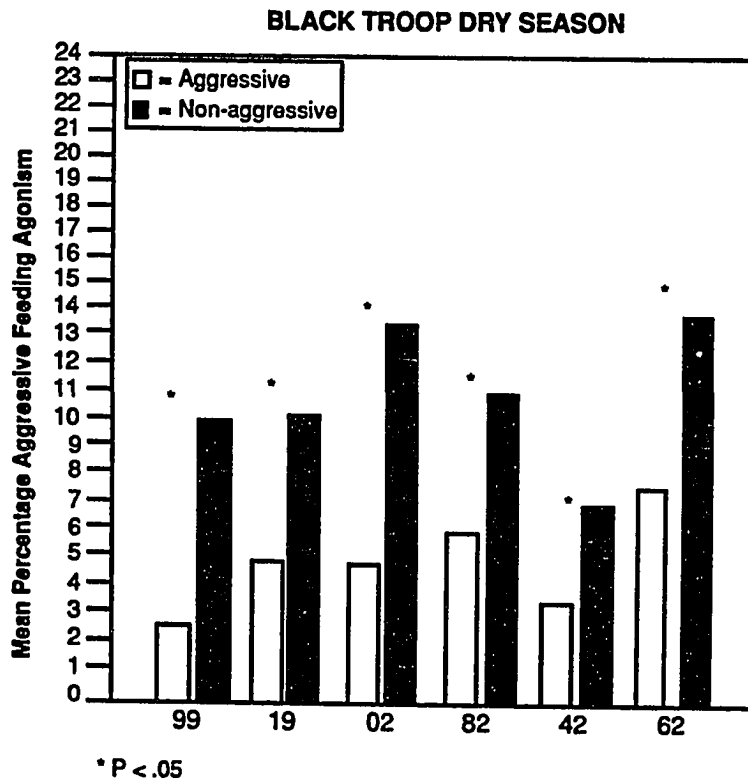
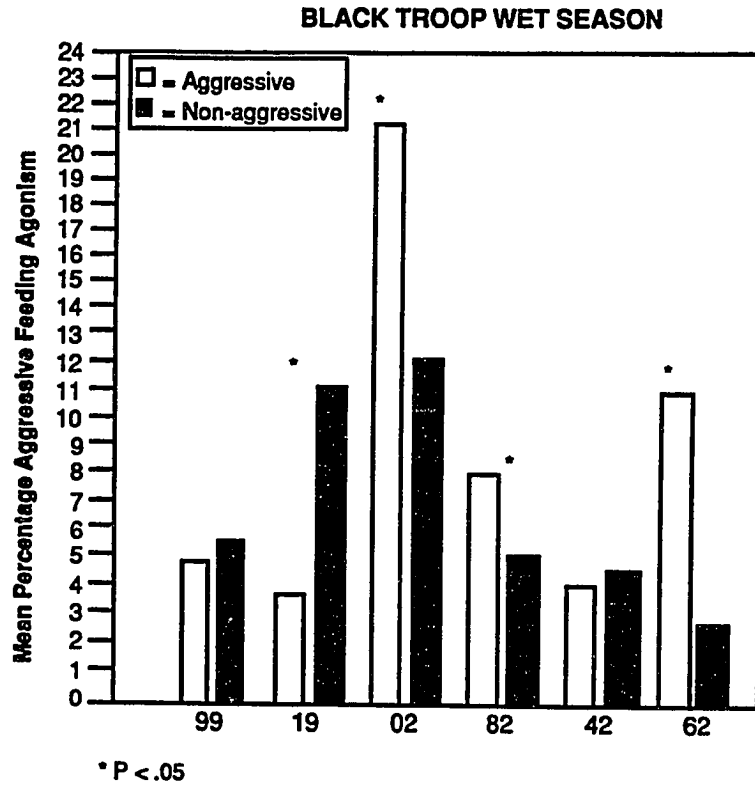


Figure 4.17. Mean Percentages of Time Involved In Aggressive versus Non-aggressive Feeding Agonism During the Wet and Dry Seasons In Black Troop.

Females versus Males

Figures. 4.18 and 4.19 compare aggressive feeding agonism involving males and females for each season in Green and Black Troop. During both the wet and dry season most females were involved in more aggressive feeding agonism than were males. During the dry season, male 19 of Black Troop, is the only male that does not clearly reflect this pattern, in part because of the high percentage of agonism he received from the central male (99 and 19 = 3%, versus 02 and 19 = 1.6%, 82 and 19 = .80%, 42 and 19 = 1.8%, 62 and 19 = 0).

WET SEASON

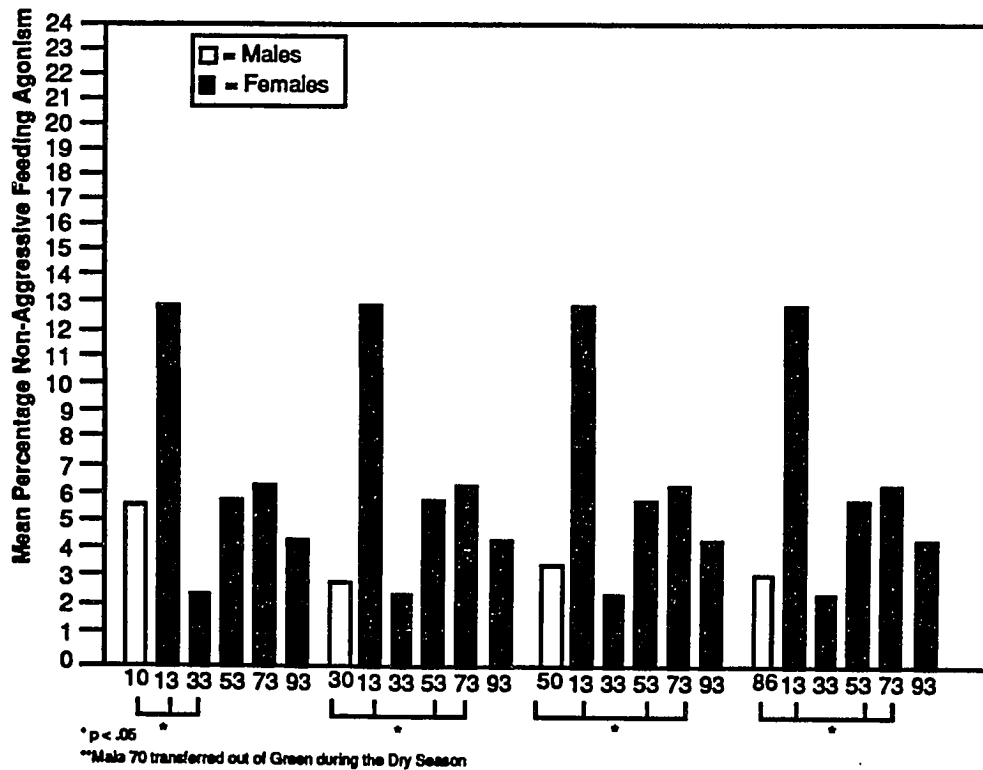
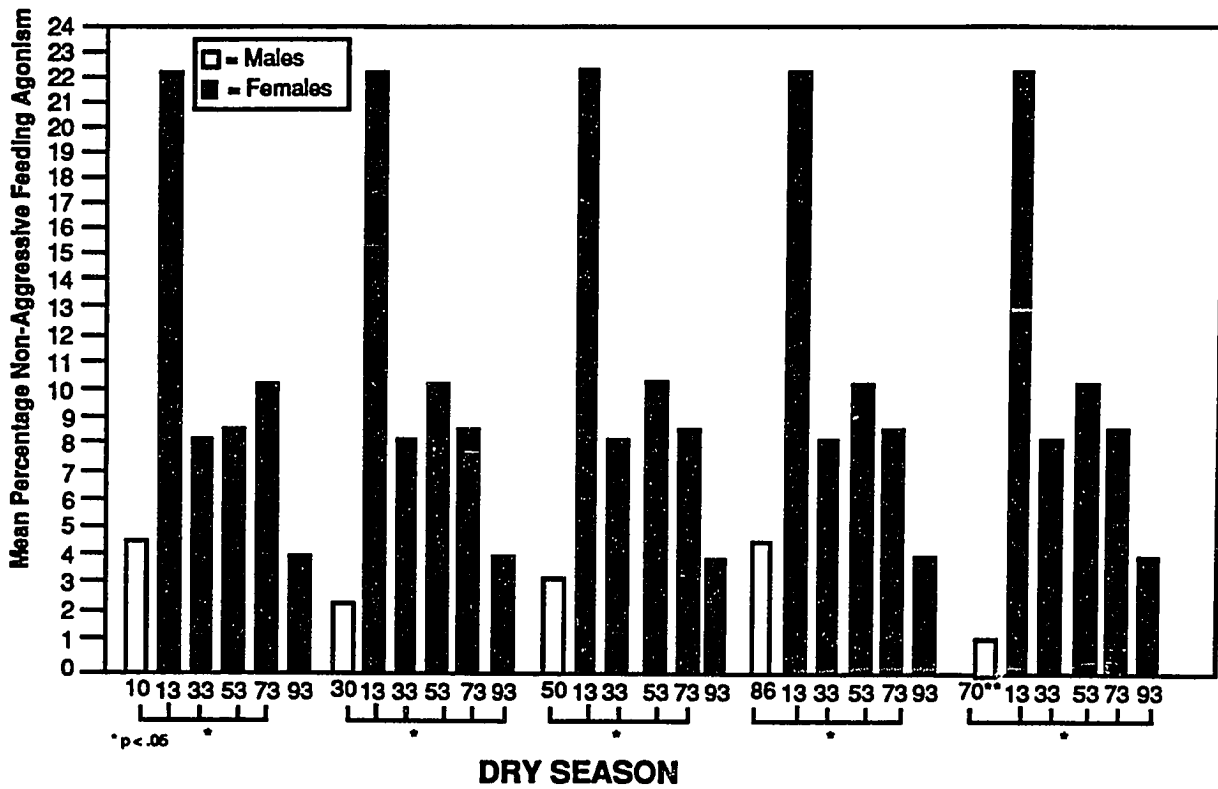


Figure 4.18. Comparison of Male and Female Mean Percentages of Time Involved In Aggressive Feeding Agonism During the Wet and Dry Seasons for GreenTroop.

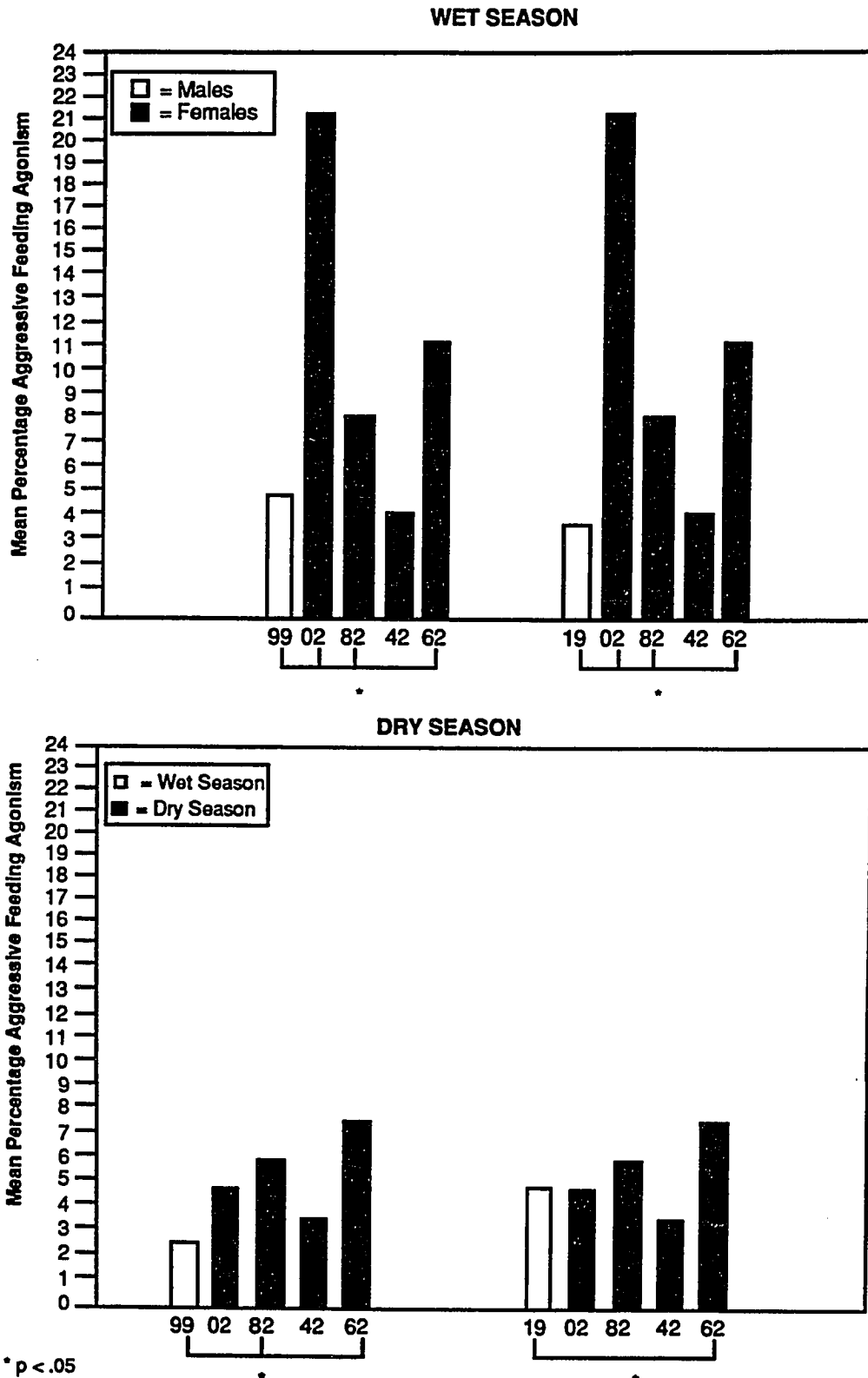


Figure 4.19. Comparison of Males and Females for Mean Percentages of Aggressive Feeding Agonism During the Wet and Dry Seasons.

Figures. 4.20 and 4.21 show nonaggressive feeding agonism for males and females. In the wet season most males had fewer nonaggressive agonistic bouts than high-ranking females. During the dry season most females, regardless of rank, were involved in more nonaggressive feeding agonism than were males.

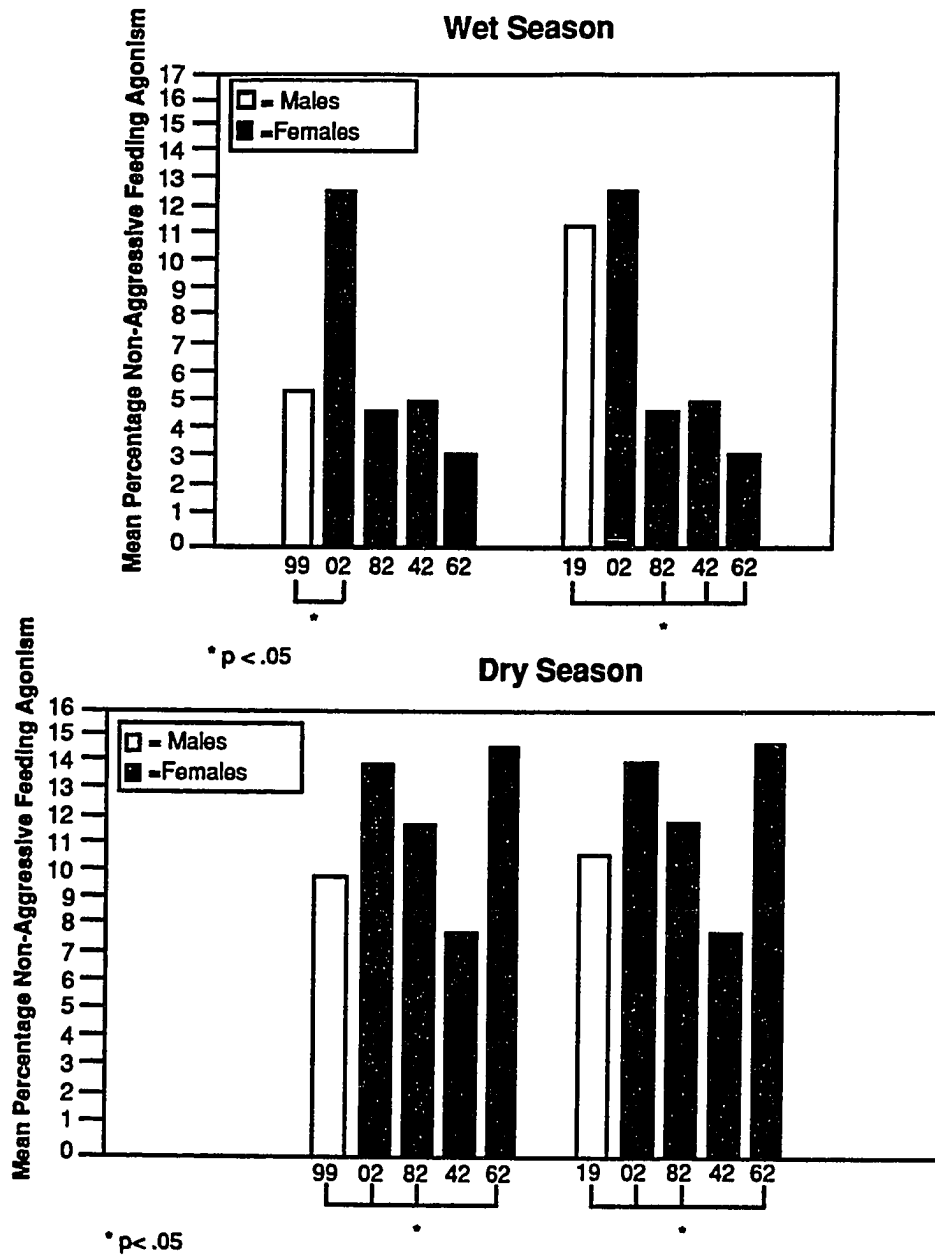
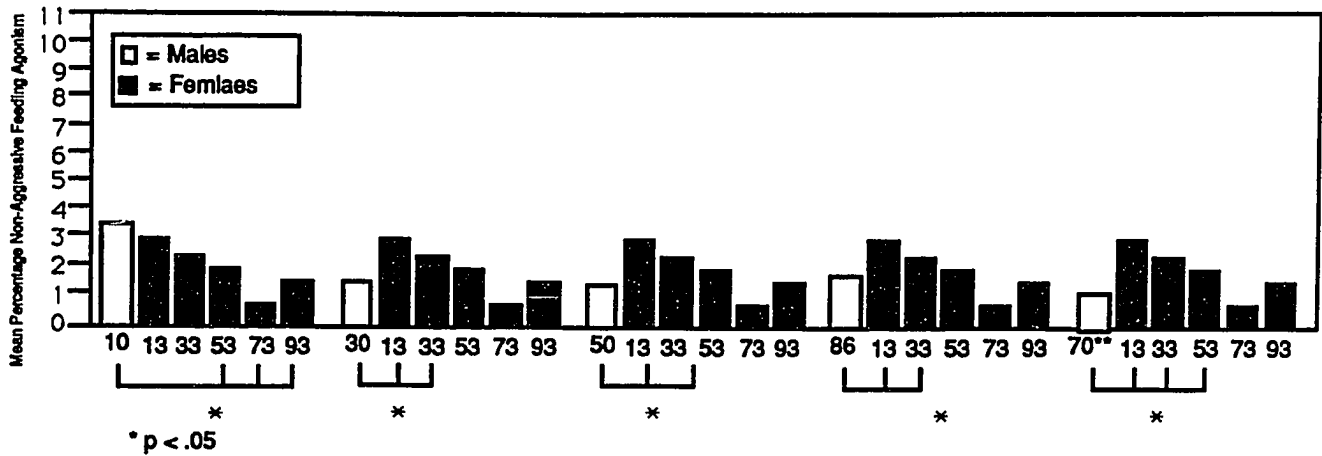


Figure 4.20. Comparison of Male and Female Mean Percentages of Time Involved In Non-Aggressive Feeding Agonism During the Wet and Dry Seasons for Black Troop.

WET SEASON



DRY SEASON

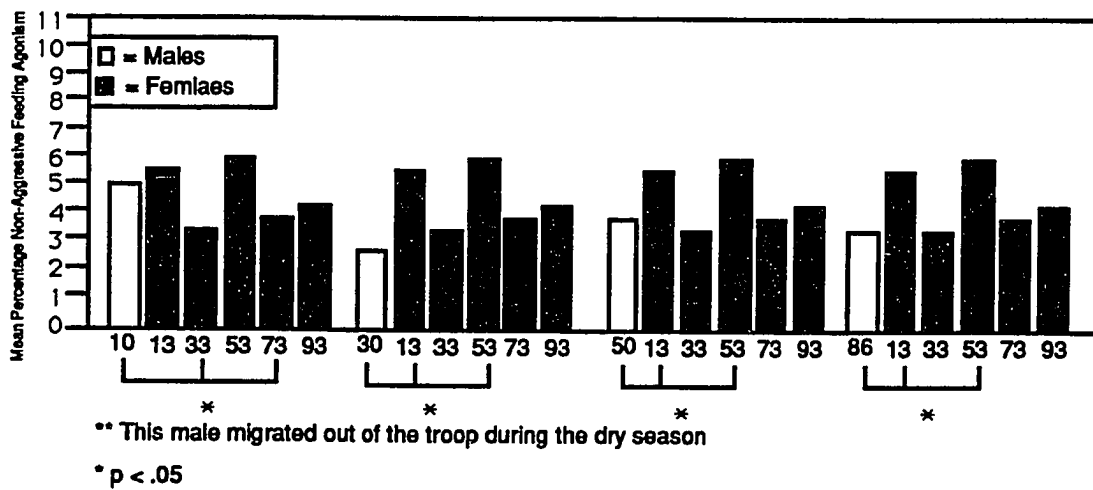


Figure 4.21. Comparison of Male and Female Mean Percentages of Time Involved In Non-Aggressive Feeding Agonism During the Wet and Dry Seasons for Green Troop.

Agonism Type and Social Rank

Tables 4.14 and 4.15 show the mean percentage of aggressive and nonaggressive feeding agonism by social rank broken down by winner and loser. Aggressive winners in feeding agonism reflected social rank, with higher-ranking females having disproportionately higher mean percentages of aggressive feeding wins regardless of season. Lower-ranking females showed higher mean percentages of aggressive feeding losses during both seasons. Indeed, some lower-ranking females suffered higher percentages of aggressive feeding agonism than even males (Wet Season: Green Troop, 73; Black, 62; Dry Season: Black, 42 and 62).

***70 migrated to Blue Troop during the Dry Season**

Table 4.15. Mean percentage of aggressive and non-aggressive feeding agonism in Black troop.

Aggressive					
WINNER			LOSER		
Female	Rank	Wet	Dry	Wet	Dry
02	1	42.50	9.06	0.00	0.00
82	2	10.80	12.02	5.20	0.80
42	3	3.80	3.78	8.30	13.80
62	4	4.00	0.00	21.80	13.80
Male					
99	5	0.48	4.18	9.20	1.60
19	6	0.40	0.20	7.20	8.80

Non-Aggressive					
WINNER			LOSER		
Female	Rank	Wet	Dry	Wet	Dry
02	1	25.00	28.60	0.0	0.00
82	2	7.90	21.06	1.60	4.80
42	3	1.40	7.36	8.80	8.40
62	4	0.60	3.30	7.70	20.00
Male					
99	5	7.12	5.50	3.20	14.80
19	6	0.40	0.0	22.00	13.20

For males, aggressive feeding agonism in the two troops showed a less consistent pattern during the wet season. In Black Troop the central male (99) and the other resident male (19) both had equally low percentages. In Green Troop, the central male (10) had higher aggressive feeding wins, but the second-ranking male (30) had none. However, central males in both troops had greater aggressive wins in the dry season.

Losses involving aggressive feeding agonism during the wet season were variable in both troops, with no clear rank effects among males. For losses during the dry season, no consistent pattern is seen for males in Green Troop, although in Black Troop the central male had fewer losses involving aggressive feeding agonism. The lack of clear rank effects and more variability among males is at least partly due to male losses involving both males and females, whereas wins among males were almost entirely with other males.

Nonaggressive wins in a feeding context more clearly reflected social rank effects for both males and females during the wet season, with lower-ranking individuals exhibiting fewer nonaggressive wins and more nonaggressive losses. Losses involving nonaggressive feeding agonism during the wet season also reflect social rank for both male and females in Black Troop, and weakly for females in Green Troop. Nonaggressive losses for Green Troop males did not reflect social rank.

Losses during the dry season clearly reflected social rank in Black Troop between females, but not between males. In Green Troop there is a weaker relationship for females and no relationship between social rank and nonaggressive losses for Green Troop males.

RANK AND FOOD INTAKE

Top 10 Foods Eaten For the Year

Table 4.16 and 4.17 show the top 10 foods (based on weight) eaten by each individual in Black and Green Troop for the year. These foods made up 66-81% (Green Troop) and 57-73% (Black Troop) of total species/parts ingested

for the year. TIFR made up the top-ranking food for all individuals, which is not surprising since this food was available and utilized all year whereas the other foods were more seasonal.

Of the top 10 foods, fruits made up a greater percentage of the diet of higher-ranking females (e.g. 13 and 33 Green Troop, 02 and 82 Black Troop), whereas leaves were fed upon more by lower ranking females. There were no apparent rank effects among males. Comparing males and females, higher- ranking females had greater percentages of fruit and lower percentages of leaves in their diet than did males. However, males and lower- ranking females showed similar percentages.

Top 20 Foods by FoodType

Table 4.16 and 4.17 lists the total weights of the top 20 foods by type for each individual in Green and Black Troop for the year. TIFR (*T. indica*) is presented separately because it was qualitatively different from other fruits. It was available year round, and it was heavier and more fibrous, and contained less water relative to other fruits, which were juicy drupes (based on percentage of water determined by weighing fruits before and after drying). TIFR was also associated with low feeding agonism. I therefore decided to present TIFR separately from other fruits, since it might mask important rank-related differences. The two top ranking females in each troop ingested more fruit, by weight, than other individuals. Among males, high rank held no advantage for fruit feeding. The lowest-ranking, most peripheral male in Green Troop (male 70), had the highest ingestion of fruits (excluding TIFR). In Black Troop there were no clear rank effects associated with total leaf feeding, but in Green Troop lower-ranking individuals ingested more leaves, by weight, than higher-ranking individuals. Among males no clear rank effects were evident. In Black Troop higher-ranking individuals ingested greater weights of flowers than lower-ranking *L. catta*. No such differences were seen in Green Troop. Lower-ranking individuals tended to feed more by weight on flowers. In Green Troop lower-ranking individuals, both males and females, had greater weights of TIFR in their diet than did higher-ranking individuals, but in Black Troop this was only the case for males.

There were no rank effects associated with total weight ingested for either troop.

Table 4.16. The Top 20 Foods (in grams) eaten by Individuals of Green troop for the year.

Individual	Rank	*FRUITS	LEAVES	FLOWERS	TIFR	Total No TIFR	Total With TIFR
13	1	4.37	2.08	.26	15.90	6.71	19.43
33	2	4.57	1.66	.30	22.26	6.53	22.43
53	3	1.80	7.44	.22	20.67	9.46	33.31
73	4	2.90	2.99	.48	22.44	6.37	30.22
93	5	3.70	3.22	.40	38.16	7.32	45.48
10	6	2.29	2.65	.28	19.08	5.22	30.66
30	7	1.74	3.18	.38	28.62	5.30	32.22
50	8	2.70	2.94	.36	12.72	6.00	26.67
86	9	2.62	3.17	.40	47.80	6.19	53.89
70	10	3.64	1.72	.36	30.21	5.72	32.75

*Does not include TIFR

Table 4.17. Total weight of the top 20 foods eaten by individuals of Black troop for the year.

Individual	Rank	*FRUITS	LEAVES	FLOWERS	TIFR	TOTAL No TIFR	TOTAL With TIFR
02	1	2.36	1.36	.70	55.65	4.42	60.07
82	2	2.45	3.28	.72	39.75	6.45	46.20
42	3	1.27	1.77	.16	20.67	3.20	23.87
62	4	1.39	2.45	.36	34.98	4.20	39.18
99	5	1.86	3.99	.28	19.08	6.13	25.21
19	6	1.46	1.82	.24	79.50	3.52	83.02

*Does not include TIFR.

Social Rank and Food Type

Table 4.18 and 4.19 shows the mean weights of the top 20 foods eaten by individuals of Green and Black Troop by rank and season. Among females during the wet season there were no consistent rank affects associated with fruit feeding (excluding TIFR) in Green troop, although in Black troop the top-ranking female (02) had greater intake. Reproductive state did appear to affect total fruit feeding, however, with lactating females (Black: 82, 42; Green 13, 53) feeding less on fruit (See also Chapter 3) due primarily to less TIFR feeding by lactating females. Total food intake, with or without TIFR also did not correlate consistently with rank during the wet season. Among males no meaningful rank effects were seen for fruit without TIFR during the wet season. However, in both troops low-ranking males fed more on TIFR than high ranking males (Black: 19; Green: 86 and 70). There were no clear rank effects for fruit feeding among males during the dry season.

Table 4.18. Mean weight of top 20 foods eaten by individuals of Black troop by season.

WET SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
02	1	1.52	6.98	8.50	.62	0	2.14	9.12
82	2	.65	5.00	5.65	1.76	0	2.41	7.41
42	3	.65	2.15	3.80	1.32	0	2.14	5.12
62	4	.67	6.04	6.71	.93	0	1.60	7.64
99	5	.94	2.86	3.80	1.68	0	2.62	5.48
19	6	.93	11.45	12.38	1.30	0	2.23	13.68

DRY SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
02	1	.20	.96	1.16	.17	1.44	1.81	2.77
82	2	.44	2.86	3.30	.08	1.08	1.60	4.46
42	3	.24	1.59	1.83	.26	.16	.66	2.25
62	4	.24	2.12	2.36	.31	.45	1.00	3.12
99	5	.08	.95	1.03	.48	.28	.84	1.79
19	6	.04	2.95	2.99	.10	.24	.38	3.33

Table 4.19. Mean weights of top 20 foods eaten by individuals of Green troop by Season.

WET SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
13	1	1.59	1.27	2.86	1.17	0	2.76	4.03
33	2	1.83	2.86	4.69	.92	0	2.75	5.61
53	3	1.08	1.59	2.67	2.51	0	3.59	5.18
73	4	2.20	3.18	5.38	1.01	0	3.21	6.39
93	5	1.71	3.49	5.20	1.09	0	2.80	6.29
10	6	1.65	.95	2.60	1.01	0	2.66	3.61
30	7	.96	3.50	5.42	1.26	0	2.22	6.68
50	8	1.91	1.27	3.18	1.38	0	3.29	4.56
86	9	1.66	6.77	8.43	1.81	0	3.47	10.24
70	10	1.72	6.16	7.88	.85	0	2.57	8.73

DRY SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
13	1	.69	1.91	2.60	.48	.26	1.43	3.34
33	2	.38	1.27	1.65	.37	.30	1.05	2.32
53	3	.88	2.23	3.11	1.22	.32	2.42	4.65
73	4	0	1.31	1.31	.63	.53	1.16	2.47
93	5	.21	4.13	4.34	.65	.60	1.46	5.59
10	6	0	2.86	2.86	.97	.42	1.39	4.25
30	7	0	2.23	2.23	.53	.67	1.20	3.43
50	8	.06	1.27	1.33	.99	.54	1.59	2.86
86	9	0	1.27	1.27	.58	.60	1.18	2.45
70	10	.77	1.91	3.95	.82	.54	2.13	5.31

During the wet season leaf feeding did not correspond with rank, but lactating females fed more on leaves. There were no rank effects among males for leaf feeding during the wet season.

Weights of fruit ingested (without TIFR) during the dry season did not correlate with rank in Black troop, but did so in Green troop. However, females in both troops had greater fruit intake, than males. Among females, total fruit intake was greatest for the daughters of the top-ranking female during the dry season (Green: 93; Black: 82). This was due to higher TIFR feeding by 93, and by higher intake of all fruits by 82.

There was a rank effect for leaf consumption among females during the dry season. Lower-ranking females had greater leaf intake than higher-ranking members. Rank effects for flowers were seen in Black Troop but not Green Troop. There were no rank effects among males during the dry season for leaf or flower feeding.

Total intake is less for lactating females, again primarily due to lower TIFR intake during the wet season. No clear rank effects were seen for total weights (with or without TIFR) during the wet or dry season. However, comparing known mother-daughter pairs during the dry season reveals that daughters (Green troop: 93, 73; Black troop: 62, 82) had higher total intake than did mothers. Furthermore, daughters of highest-ranking females had the greatest total intake relative to females and most males. Mother-son pairs (33 and 86) did not show this pattern.

Rank Effects Associated with Specific Foods

Tables 4.20 and 4.21 show the mean weights in grams for particular fruit and leaf species consumed by each individual. Among Green Troop females, female 93, the lowest-ranking female, had the greatest intake of TIFR (fruits of *Tamarindus indica*). Among males, lower-ranking individuals had greater intake of TIFR than higher-ranking males during the wet season (Wet Season, Green Troop: 86, 70; Black Troop: 19; Dry Season, Black Troop: 19).

Table 4.20. Mean weights in grams of selected fruits and leaves eaten by Black troop.

Individual	Rank	TIFR*	TIFR	03FR	QUFL	SAFR	APFR	G4FR	TILB	MCLV	TALV	ESFR	AMLV
02	1	6.67	.95	.01	.05	.05	.03	.22	.03	.01	0	.064	.84
82	2	5.00	2.86	.003	.09	.06	.01	.03	.03	.02	.02	.088	0
42	3	2.05	1.59	.005	.02	.01	.05	0	.02	.02	.01	.072	.49
62	4	6.05	2.12	0	.02	.03	0	0	.02	0	.0006	.080	.14
99	5	2.06	.95	.003	.02	.03	.006	.26	.02	.0001	.02	.04	.49
19	6	11.45	3.50	0	.01	.03	.14	0	.01	.002	.008	.008	.98
$\bar{X}$		5.56	2.63	.004	.04	.04	.04	.09	.02	.008	.009	.06	.49

*See table 1.1 for complete plant names.

Table 4.21. Mean weights in grams of selected fruits and leaves eaten by Green troop.

Individual	Rank	Wet Season		Dry Season		Wet Season		Birth Season		Wet Season		Birth Season		Wet Season		Birth Season		Wet Season		Dry Season	
		TIFR	TIFR	TAFR	03FR	QUFL	G6FR	SAFR	TILB	MCLV	TALV	GAFL	ESFR								
13	1	1.27	1.90	.03	.06	.07	2.32	.15	.01	.03	.05	.01	0								
33	2	9.86	1.29	.04	.02	.06	1.95	.08	.008	.0009	.02	.02	.008								
53	3	1.59	2.22	.02	.02	.03	.22	.08	.01	.03	.05	.01	.020								
73	4	3.18	1.30	.05	.02	.07	.80	.09	.004	.0009	.03	.007	.020								
93	5	3.50	1.30	.07	.03	.08	1.10	.10	.02	.03	.03	.01	.056								
10	6	.95	4.13	.07	.02	.06	1.24	.05	.009	.01	.02	0	**								
30	7	3.49	2.86	.04	.0009	.06	1.59	.05	.02	.01	.03	.02	**								
50	8	1.27	1.27	.06	.03	.06	1.06	.07	.005	.01	.01	0	.01								
86	9	7.57	1.90	.03	.0007	.05	.80	.12	.006	.02	.0008	0	**								
70*	10	3.49	*(1.90)	.15	.02	*(.05)	.53	*(.11)	.02	.02	.04	0	*(.05)								
$\bar{X}$		2.95	2.03	.06	.02	.06	1.16	.09	.01	.02	.03	.008	.01								

*70 migrated to Blue Troop during the Dry Season

**This food was not eaten by these individuals during focal samples.

No rank effects were seen for ingestion of TAFR (*Talinella dolphinensis* fruits). In both troops the highest-ranking female had higher mean weights of 03FR (*Grewia clavata* fruits) consumption ($P < .05$), but there were no rank effects among the other females. Similarly, the consumption of other *Grewia* fruits (G6fr: *Grewia leucophylla*, and G4fr: *Grewia triflora*) was associated with rank effects, with higher weights ingested by both high ranking males and females. The only exception was female 93, the daughter of 13, who had higher minimum weights than expected based on her rank (see chapter 6).

There were rank effects only for Black Troop with respect to QUFL (*Quisivianthe papinae* flower) with higher ranking females (02 and 82) feeding more on this food item. For SAFR (*Salvadora augustifolia* fruits) there were some rank effects. In Green Troop the top-ranking female (13) fed more on this food item than other members. In Black Troop the two highest-ranking females also fed more on SAFR, but no other rank effects were evident. APFR (fruits of *Antidesma petiolare*) were eaten only by Black Troop, and no rank effects were seen for this food. For GAFL (*Gyrocarpus americanus* flowers) Green Troop females fed more on GAFL than did most males (only one male fed on this food item during focal samples). A similar pattern is seen for ESFR, as females again fed more on this item than most males. No rank effects were seen for any species of leaves (TILB: *T. indica* leaf buds; MCLF: young leaves of *Hildebrandtia* sp., TALV: young leaves of *Talinella* sp, although again lactating females fed more on these specific leaves during the wet season than most other females (see Chapter 3). This does not mean that feeding displacements did not occur over leaves. For example, small patches of the herb, *Hildebrandtia*, often could not accomodate all individuals and males would wait for females to finish. But overall, this did not result in rank differences between males and females perhaps because such food was not visibly depleted by females.

The Agonistic Index and Rank Effects

Table 4.22 compares the agonistic index for foods with the presence or absence of rank effects. The agonistic index was determined as the percentage of agonism over a given food + by the percentage of time spent feeding on the same food, with 1 indicating that the individual was involved in the same amount of agonism as time spent feeding on the item. The higher the index, the greater the agonism, relative to feeding, and vice versa. G6FR (eaten primarily by Green Troop) and 03FR, eaten by both troops, are characterized by both a high agonistic index and social rank effects, with high ranking individuals spending markedly more time feeding on these fruits. APFR (eaten by Black Troop only) and TAFR (eaten only by Green Troop) have a relatively high agonistic index but no rank effects. SAFR has a low agonistic index but limited rank effects in that in both troops the top-ranking females spent significantly more time feeding on SAFR than lower-ranking females. QUFL shows a low agonistic index and a rank effect in Black troop, but not in Green Troop. ESFR has a low agonistic index but shows a rank effect in that females feed more on this fruit than did males. TIFR shows a low agonistic index and no rank effect for both troops. GAFL has a relatively higher agonistic index and rank effects among males and females. Of the leaf resources, TILV and MCLV were associated with the lowest agonistic index and no rank effects, but AMLF had a higher agonistic index and no rank effects.

Table 4.22. Relationship between the agonistic Index and rank effects in Black and Green troop.

BLACK TROOP

FOOD	¹ AGONISTIC INDEX	RANK EFFECT
APFR	1.51	no
03FR	2.16	yes
³ TIFR	.53	no
³ QUFL	.22	yes
³ SAFR	.42	highest ranked female
G4FR	2.00	yes
ESFR	.78	females more than males
AMLF	.65	no
TILF	.09	no

³ Significantly less than APFR, G4FR, and 03FR at $p < .05$

GREEN TROOP

FOOD	¹ AGONISTIC INDEX	² RANK EFFECT
APFR	-	-
03FR	2.34	yes
⁴ TIFR	.90	no
⁵ QUFL	.24	no
⁵ SAFR	.58	highest ranked female
G6FR	1.68	yes
TAFR	1.08	no
GAFL	.82	females more than males
ESFR	.86	females more than males
MCLV	.41	no
TILV	.21	no

¹ Agonistic Index = percentage of agonism over a given food ÷ percentage time spent feeding on the same food. The higher the index, the greater the agonism, relative to feeding.

² "Rank Effect" refers to whether higher ranking individuals fed more on that food item.

⁴ Significantly less than G6FR, G4FR and 03FR at $p < .05$

⁵ Significantly less than TAFR, G6FR, GAFL, G4FR and 03FR at $p < .05$

FEEDING EFFICIENCY

Specific Foods

To determine the feeding efficiency of specific foods, a ratio was made which was the percentage of time spent feeding on species A + time spent foraging for species A. These results are presented in Table 4.23 and 4.24. The higher the ratio, the more time spent feeding relative to foraging. No consistent patterns associated with rank are seen for efficiency in TIFR feeding. However, during the dry season for Green Troop and the wet and dry season for Black Troop the daughters of the highest-ranking females (Green Troop: 93; Black Troop: 82) have the highest efficiency ratio, higher than all other females and most males.

Table 4.23. Feeding efficiency ratio for specific foods for Individuals of Green troop for the year.

GREEN TROOP

Individual	Rank	TIFR WET	TIFR DRY	SAFR	03FR	TAFR	G6FR	QUFL	GAFL	ESFR
13	1	2.00	.36	2.46	.70	7.00	.76	3.25	1.00	.001
33	2	1.25	.27	.88	.47	4.20	.69	15.00	2.00	.33
53	3	4.00	.33	1.05	1.00	1.12	1.00	5.50	3.00	.66
73	4	1.09	.22	.96	.75	2.45	.80	3.00	1.00	..**
93	5	1.83	1.63	2.67	1.80	2.38	.60	3.33	1.00	3.50
10	6	.85	1.00	.44	.44	3.00	.84	1.75	..**	..**
30	7	1.50	.50	.39	1.00	1.67	2.00	2.38	1.00	.001
50	8	1.00	.18	.50	3.33	2.67	.44	6.00	.0001	.40
86	9	.80	.66	1.85	.20	1.58	.50	2.22	.0001	..**
70	10	3.00	.40	.69	2.42	5.14	2.00	3.00	..**	.16
$\bar{X}$		1.73	.56	1.19	1.21	3.12	.96	4.54	1.20	.51

*Ratio of 1 = equal time spent feeding and foraging. The higher the ratio, the more time spent feeding relative to foraging, i.e. more "efficient".

**These Individuals were not recorded feeding on this food item.

Table 4.24. Feeding efficiency ratio for specific foods for individuals of Black troop for the year.

BLACK TROOP

Individual	Rank	TIFR WET	TIFR DRY	SAFR	03FR	QUFL	APFR	ESFR
02	1	2.00	.12	.71	.71	2.07	3.00	2.66
82	2	4.75	.54	1.88	.14	8.75	1.33	.92
42	3	.53	.33	2.00	1.00	8.00	2.00	4.50
62	4	1.72	.20	8.00	0	6.00	0	1.25
99	5	4.33	.11	.85	.50	3.50	1.00	1.25
19	6	3.60	.48	.57	.001	2.40	4.00	.33
$\bar{X}$		2.82	.30	2.34	.39	5.11	1.88	1.82

*Ratio of 1 = equal time spent feeding and foraging. The higher the ratio, the more time spent feeding relative to foraging.

In Green Troop the efficiency ratio for SAFR is greatest for the top ranking female and her daughter. In Black Troop this is not seen. Among males, 86, the son of the female 33, (second-ranking female) showed the highest feeding ratio for this food.

No consistent rank effects were seen for the efficiency ratios of 03FR. However, in both troops when high ratios are seen they occur among lower-ranking females or among males. A similar pattern occurred with G6FR.

TAFR efficiency was greater among high-ranking females in Green Troop (females 13 and 33) and for the central male compared to most other males.

No clear rank effects could be associated with QUFL efficiency in Green Troop. However, in Black Troop the highest-ranking female had a lower efficiency ratio than all other individuals. APFR was associated with rank effects in that the top-ranking female had a higher efficiency ratios for this

food than most other members. ESFR efficiency was not associated with rank effects.

Overall Feeding Efficiency Ratios

How does this translate into overall efficiency ratios? In Table 4.25 the feeding efficiency ratios for the two troops is shown. The higher the ratio, the more time the individual spends feeding relative to foraging. For both troops the top-ranking female shows the lowest feeding efficiency during the wet season ($p < .05$, all dyads involving female 13 of Green Troop, except 13 and 50, and female 02 of Black Troop, except 02 and 99). Among males, lower-ranking individuals have greater feeding efficiency ratios than higher-ranking males.

Table 4.25. Feeding Efficiency Ratio for Green and Black Troop.**BLACK TROOP**

Individual	Rank	Wet	Dry
02	1	.75	.42
82	2	2.90	.67
42	3	1.15	.81
62	4	1.65	.69
99	5	.35	.35
19	6	6.00	.58

GREEN TROOP

Individual	Rank	Wet	Dry
13	1	.89	.53
33	2	1.38	.32
53	3	1.33	.44
73	4	1.20	.34
93	5	1.40	2.09
10	6	1.57	1.08
30	7	1.25	.44
50	8	.91	.22
86	9	3.52	1.00
70	10	3.12	1.30

*Ratio of 1 = equal time spent feeding and foraging. The higher the ratio, the more time spent feeding relative to foraging.

During the dry season all individual's feeding efficiency was dramatically reduced relative to the wet season ($p < .05$ for all individuals except male 10) indicating that all troop members were foraging more to find food. Again the top-ranking female in Black troop has the lowest feeding efficiency ratio, superseded only by male 99. In Green troop this is not seen as the top-ranking female and her daughter (13 and 93) have the highest feeding efficiency ratios among females. During the dry season most males have efficiency ratios that are equal to or greater than ratios for most females.

NUMBER OF SPECIES USED

The mean number of species used by individuals during the wet and dry season is presented in 4.26. Overall, lower-ranking individuals tended to use a higher number of species than higher-ranking ringtailed lemurs. This is true during the wet (Green Troop) and dry (Green and Black Troop) season for females and the wet (Green Troop) and dry (Black Troop) season for males.

Table 4.26. Mean number of species used by individuals of Black and Green troop.**BLACK TROOP**

Individual	Rank	Wet	Dry
02	1	6.4	4.4
82	2	6.4	2.8
42	3	5.0	6.0
62	4	6.6	6.4
99	5	4.4	4.4
19	6	4.8	6.0

GREEN TROOP

Individual	Rank	Wet	Dry
13	1	6.6	4.0
33	2	5.4	3.3
53	3	7.4	6.0
73	4	7.0	5.0
93	5	6.2	5.4
10	6	5.8	4.8
30	7	5.0	3.2
50	8	4.4	4.4
86	9	7.4	4.6
70*	10	8.6	5.4

*70 migrated to Blue Troop during the Dry Season

DIETARY OVERLAP: RANK EFFECTS

Table 4.27 shows dietary overlap for both troops. Among males, in both troops the central males (Green: 10; Black: 99) showed a greater dietary overlap with females than did other males during the wet season. Interestingly, male 60 who unsuccessfully attempted to transfer into Green Troop shows a similar dietary overlap as other males, even though he remained peripheral throughout the period. His overlap with other males was greater than the most peripheral troop male 70. He also showed an equal or greater overlap with females, compared to troop male 70.

No rank effects for dietary overlap were evident among females during the wet season.

During the dry season higher-ranking males continued to display a greater dietary overlap with troop females, although in this case it was the second-ranking male (30) in Green Troop who showed this pattern. The central male of Black Troop (99) continued to show higher overlap with his troop's females than the other, more peripheral male (19).

Lower-ranking females in Green troop (73 and 53) had less dietary overlap with other females and males during the dry season. This was less dramatic for female 93 due to her high overlap in diet with her mother, female 13. In Black troop the lowest-ranking female, 62, had a similar dietary overlap as other females due to the high overlap between her and her mother, 42.

During the birth season most males show a greater dietary overlap with other females than with each other. In both troops the lowest-ranking females (Green Troop: 93; Black Troop: 62) have the lowest dietary overlap with other females.

Table 4.27. Mean Dietary Overlap in Black and Green Troop.

WET SEASON			DRY SEASON		BIRTH SEASON	
Individuals	Overlap with females	Overlap with males	Overlap with females	Overlap with males	Overlap with females	Overlap with males
02	.55	.40	.40	.40	.57	.40
82	.48	.45	.40	.38	.48	.45
42	.52	.66	.50	.54	.52	.66
62	.40	.48	.54	.54	.40	.48
99*	.53	.36	.52	.43	.53	.40
19*	.47	.36	.40	.43	.47	.40

*Because there were only two troop males the proportions for "overlap with males" is a single proportion.

WET SEASON			DRY SEASON		BIRTH SEASON	
Individuals	Overlap with females	Overlap with males	Overlap with females	Overlap with males	Overlap with females	Overlap with males
13	.38	.42	.37	.46	.46	.46
33	.49	.51	.42	.35	.40	.41
53	.36	.46	.25	.38	.44	.56
73	.46	.58	.27	.19	.40	.41
93	.44	.33	.32	.43	.25	.35
10	.61	.51	.31	.34	.37	.34
30	.42	.41	.51	.61	.44	.34
50	.50	.40	.34	.54	.43	.34
86	.41	.50	.29	.56	.34	.28
70	.42	.48	-	-	.57	.35

*This individual transferred to Blue Troop during the dry season.

DISCUSSION

FEEDING COMPETITION

Feeding Competition and Reproductive State

If feeding competition can limit female (and less directly, male) reproductive success (Loy, 1988; Lyles and Dobson, 1988, Dittus, 1980), then individuals should be expected to minimize feeding costs whenever possible. Due to the relatively higher costs associated with lactation one should expect this class of females to forage in such a way as to lessen feeding costs. Maintenance of greater interindividual distances when feeding and foraging have been associated with a reduction of feeding agonism (Mori, 1977; Furuichi, 1983). From the perspective of minimizing foraging costs during lactation, feeding farther from others would potentially reduce contest competition. Furthermore, females should avoid feeding near other individuals with similar dietary requirements (Robinson, 1981) especially during a costly reproductive state such as lactation. In Chapter 3 it was noted that lactating females focused on foods that were less costly in terms of foraging and contest competition (e.g. leaves). In this chapter lactating females spent more time feeding alone, and avoided one another as nearest neighbors. This is most likely related to their higher incidence of feeding on dispersed resources such as leaves (see Chapter 4). Taken as a whole, the common premise that lactating females suffer the greatest potential feeding cost is reflected in feeding and foraging behavior that seems designed to lessen these same costs.

Pregnancy occurred during the cooler dry season, when food availability drastically decreased. Females were thus contending not only with gestation but reduced resources. As in lactation, under these circumstances one might expect females to increase solitary feeding and reduce their percentages of female nearest neighbors, since other females would have similar dietary requirements. For example, van Noordwijk and van Schaik (1987) noted that low-ranking long-tailed macaques (*Macaca fascicularis*) spent more time

solitary or in smaller sub-groups. They suggest this was a way for low-ranking individuals to avoid feeding competition with high-ranking females over clumped fruit resources, although they did not present direct data on fruit use. In this study there were no clear patterns between rank and solitary feeding, although as a whole, troop members reduced solitary feeding in the dry season relative to the wet season. For these troops the availability of food and its distribution affected the spatial relationships of individuals as they fed. During the dry season food availability was reduced and consisted primarily of occasional patches of herbaceous leaves or TIFR which were found in large trees or on the ground beneath a *T. indica* tree. The available foods in the dry season were thus less dispersed in the environment, resulting in a reduction of solitary feeding and an increase of close (<1 - 3 m) nearest neighbors.

There was also no evidence that pregnant females were avoiding one another during feeding as lactating females had done. Given the proposed constraints that food distribution in the dry season placed on pregnant females, these females could still modify contest competition by feeding near members who could be displaced by the individual. For lower-ranking females this was a male, for higher ranked females this was a lower-ranking female or male.

Hrdy's Model of Female Dominance

Hrdy (1981) has proposed one reason for female dominance in some polygynous species. She reasons that due to an interplay between small body size and seasonal restriction on food availability, males should concentrate on conserving energy and employ 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.

Lemur catta has been presented as a species which seems to fit Hrdy's model (Jolly, 1984). Under such a scenario, male ringtailed lemurs should be expected to 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. Results from this study do not support this model for numerous reasons. First, for males, rank-related advantages were not limited solely to the breeding season. High-ranking, central males spent less time using more expensive forms of locomotion, they had greater access to drinking sites than lower-ranking males, they won higher percentage of agonistic bouts over food, and they had higher rates of ingestion for clumped, defensible fruit sources. Most important, from the perspective of male reproductive success, high-ranking central males were able to spend more time monitoring the troop female's reproductive state, and they were able to keep other males away from females, enabling them to be the first to mate (Sauther, 1991). The latter is especially key as there may be a first mate advantage in this species (Pereira and Weiss, 1991). Second, male-male agonism does not support the contention that males were "saving themselves" during the lean period. Male ringtailed lemurs actually had significantly greater mean percentages of feeding agonism during the lean dry season than the wet season (3.08% versus 1.24%; Table 4.11), and maintained similar levels of aggressive feeding displacement, regardless of season. Furthermore, nonfeeding agonism remained at the same level during the wet and dry seasons. Third, there is no indication of male "chivilary" (sensu Jolly, 1984) with regards to lessening female feeding pressure. Overall, the percentage of feeding agonism between males and females remained the same during both seasons, and relative mean percentages of female-male agonism increased, although not markedly, during the dry season. Furthermore males became less peripheral during the dry season, creating more potential feeding competition for low-ranking females, who they tended to feed near.

Female Dominance and Feeding Competition

In Chapter 3, I argued that female dominance in ringtailed lemurs can best be understood as a response to high pre- and post-natal maternal investment which is set against close reproductive synchronicity and an extremely seasonally fluctuating resource base. If this is the case, then 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) then females should be willing to expend more energy in the acquisition of it. This should hold true for all primate females. However, in most species, females face contest competition not only from other females, but from larger, dimorphic males who have priority of access to resources over females. It is thus more difficult to quantify female feeding investment in such species. In ringtailed lemurs the situation is slightly less complicated because females have feeding priority over males, and there is limited body size dimorphism. Gender differences in the type of feeding aggression among ringtailed lemurs support the thesis that females show greater feeding investment than do males. For both seasons female-female and male-female feeding agonism was higher than male-male feeding agonism. Females were also involved in more expensive forms of contest competition such as chasing, cuffing and biting. Females were also the main participants in intertroop agonistic encounters over food resources (see Chapter 5).

In addition, females were under more potential feeding pressure than were males. Aside from reproductive costs, females also had higher percentages of close (<01-03m) nearest neighbors during feeding in the wet season than did males, and they had equally high percentages of close nearest neighbors regardless of the season. In the wet season this was most likely due to the tendency for close kin to feed near one another. During the dry season, close kin tended to avoid one another as close feeding partners and the high percentages of close neighbors were a result of males feeding nearer the main body of females. 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). Lower ranking females also faced increased feeding competition from males during the dry season, when males tended to feed closer to lower-ranking females. This resulted in an increase of feeding agonism directed at males by low ranking females. Males, on the other hand, could alleviate some feeding pressure by feeding further away from others during the wet season, where they could seek out more displaced foods, and during the dry season males still had greater percentages of more distant nearest neighbors.

Ringtailed lemur females thus responded to greater feeding pressures, as well as to reproduction during periods of fluctuating resource availability, by exhibiting greater feeding investment which took the form of aggressive contest competition. It can thus be argued that female dominance in ringtailed lemurs is at least a partial response to females not only competing among one another for limited resources, but facing periods where increased potential for male feeding competition coincides with periods of lowest food availability, i.e. the dry season. During such periods all females are impacted, but lower-ranking females face dual competition from both males and higher-ranking females. For such females, and their just weaned infants, female feeding priority may be especially critical.

DISTRIBUTION OF RESOURCES AND RESOURCE COMPETITION

Rank Effects

The distribution and availability of resources has an important effect on the expression of resource-related agonism. Clumped resources have been associated with some rank advantages in both provisioned and free-ranging primate species. Whitten found high rank affects only when foods, such as *Acacia tortilis* flowers, were clumped Altmann and Muruthi (1988) reported clear rank effects, with high ranking baboons spending more time feeding at a garbage dump near a tourist lodge. Brennan and Anderson (1988) showed that under artificial feeding situations, high ranking rhesus macaques fed sooner and ate more when food was in a single, monopolizable clump, and that low ranking individual's success improved when three piles rather than 1 pile were available. Barton (1988) found that the level of contest competition among free-ranging olive baboons appeared greater in the dry season when resources were more clumped. Iwamoto (1987) noted that high ranking Japanese macaque females had longer feeding bouts on provisioned foods which were clumped and monopolizable. Conversely, when food is distributed in widely spaced patches large enough to accomodate group members without crowding (> 5 m between neighbors) no dominance effects are expressed among free-ranging Japanese macaques, even though such effects are clearly noted when this species is provisioned (Furuichi, 1983). Janson, (1985a) also noted that intragroup competition was affected by

resource distribution and abundance in wedge-capped capuchin monkeys. Small and scarce resources (*Astrocaryum* inflorescence, *Scheelia* fruit clusters) engendered high feeding aggression, but dispersed resources (*Astrocaryum* seeds and *Scheelia* frond pith) did not. Furthermore, when *Scheelia* fruit clusters were less available, high rank was correlated with greater food intake, but in the wet season when this fruit was more abundant this correlation disappeared (Janson 1985a).

For ringtailed lemurs, the distribution and availability of resources affected distances between nearest neighbors during feeding. In the wet season, when food resources were more abundant and more varied, all troop members tended to disperse, but in the dry season when foods were limited both in availability and distribution all members fed closer to one another.

The distribution of water sources also affected the expression of high-rank advantages. High ranking individuals spent more time drinking, specifically when the troop drank water from tree hollows. This was a difficult procedure as such hollows tended to be on the vertical face of a tree, and often only one branch was available to sit on. The animal then had to insert the hand into the hole and reach down, immersing the hand in the collected water which the lemur would then lick. Only one individual could drink at a time, and often the water was depleted by the time lower-ranking individuals acquired access to these sites. Wrangham (1981) also noted a high rank advantage associated with drinking water from tree holes among vervet females. High ranking females could also use water sources near sleeping areas, but lower-ranking individuals had to travel farther.

High ranking males were able to spend similar or greater time drinking at tree hollows than some low-ranking females. These males often searched for alternative tree hollows (an energy expensive process), and also during the wet season were able to nonaggressively displace young adult females from these sites by simply moving the younger females aside. Due to the precariousness of this position it was difficult for these females to retaliate. Males were never seen attempting this with older adult females.

As noted by Sussman at Berenty (1972) ringtailed lemurs had alternative sources of water in the form of dew on leaves, drinking water directly from puddles in the road or the riverbed, or drinking water caught in abandoned giant snail shells. No rank effects were associated with these more dispersed water sources. This follows the general trend between rank effects and clumped food resources found in other studies (e.g. Whitten, 1983).

The severity of feeding agonism varied by season and was also most likely tied to resource type and distribution. Higher percentages of aggressive feeding agonism occurred among females during the wet season, when fruit intake was higher. Fruit feeding was associated with greater levels of both types of feeding agonism, as Table 4.30 shows. Fruit distribution in the wet season either favored larger numbers of individuals feeding near one another, creating an environment in which greater agonism could and did occur (e.g. APFR, TAFR), or were single, monopolizable resources aggressively defended by higher-ranking females (e.g. *Grewia sp.*). Greater rates of agonistic interactions during fruit feeding has also been noted for Black spider monkeys, *Ateles paniscus chamek*, at rates almost twice as high as other contexts (Symington, 1988). Resource distribution also effected rates of feeding agonism in free-ranging brown capuchin monkeys (*Cebus apella*) (Janson, 1985a). Scarce foods which occurred in small trees were associated with greater levels of feeding agonism, whereas more abundant resources showed far less feeding agonism.

Table 4.28. Comparison of the mean percentage of aggressive and non-aggressive agonism for food types in both troops.

FOOD TYPE	AGGRESSIVE	NON-AGGRESSIVE
FRUIT	47%	30%
LEAVES	9%	8%
FLOWERS	2%	4%

The distribution and type of resource appeared to limit aggressive feeding agonism in the dry season. During this period, individuals had equal or greater percentages of nonaggressive feeding agonism. As noted before, most available foods were either patches of herbaceous leaves which were associated with less aggressive feeding displacements (Table 4.28), or the pods of *T. indica* (TIFR). TIFR tended to be dispersed on the ground under a TIFR tree. Thus an individual could give up a feeding spot but still retain the pod, and this may be related to the higher incidence of nonaggressive feeding displacement.

It is difficult to discretely categorize food patches primarily due to the fact that identical food types were distributed differently in different areas. Hence QUFL was single or several trees in Black's home range, but a grove in Green troop's home range. Similarly, some patches of MCLV were large enough to support the entire troop, but other patches were much smaller. No attempt was therefore made to define patches as strictly clumped or dispersed. Instead I describe the general distribution for each food resource.

For ringtailed lemurs the type and distribution of resources also explains why some resources were associated with high rank advantages and greater or lesser feeding agonism. Both 03FR and G6FR (*Grewia* sp.) were associated with a high rank feeding advantage, and a high agonistic index. These species were small crowned trees, 7-8 meters tall, and were distributed in the reserve as single trees. Fruits from these trees were small (1 cm) single drupes which required the individual to move rapidly from one area of the tree to the next. Ripe fruits of any one tree were available for only a limited time (approximately 1 week). The lemurs clearly knew the location of these individual trees, and would travel to such sites without stopping to browse at food patches along the way. This began in January, and appeared to be monitoring behavior, as the trees were periodically checked for the presence of ripe fruit. Once the highest-ranking female arrived, she entered the tree and would only tolerate her offspring, although other individuals would continuously attempt to enter the tree to feed. These trees were thus small enough to be completely monopolizable by the top-ranking females, and these fruits are associated with clear rank effects.

Similarly, SAFR was associated with a high rank feeding advantage for the top ranking female in each troop, but had a low agonistic index. This is a species which occurs only in the drier portion of the reserve and is a large canopied tree approximately 8 meters in height. Trees are scattered throughout this area. Fruits are highly seasonal in this species, with ripe fruit being available for only a 1-2 week period. Many single trees were small enough to maintain single access. However troop members would spread out to feed in individual, widely spaced trees. Thus SAFR was associated with a rank advantage in that a single top-ranking female could monopolize access to her own tree, but low agonism as individuals could move to other trees in the area if they were displaced.

APFR and TAFR were both associated with a relatively higher agonistic index but no rank effects. Both of these species were large crowned trees 4 meters tall, and occurred in distinct, tight groves of 6-10 individual trees. The distribution and characteristics of this fruit are quite different from that of 03FR and G6FR described above. Both APFR and TAFR were like grapes, with many fruits on a single cluster so individuals did not have to move so rapidly from one feeding site to another. In addition single trees were not easily monopolized, and thus the whole troop could feed together. High rank held no advantage but the close proximity during feeding resulted in greater feeding agonism.

QUFL was associated with a low agonistic index in both troops, but rank effects occurred only in Black Troop and may be related to tree distribution. This was a large canopy species 9 meters or more in height. QUFL trees were distributed differently in Black Troop's home range when compared to the home range of Green Troop. In Black Troop these trees occurred as one or two individual trees which were widely spaced from one another. All individuals fed in one tree and if an individual was displaced there were no alternative trees in which to feed. In Green Troop, there was a single grove containing 10-11 trees in Green Troop's home range. All individuals in Green Troop would feed at the same time, as they could move to another tree if displaced from a current one. One of the few instances in this study of *L. catta* travelling in trees occurred at this grove.

ESFR was associated with a low agonistic index, but did show a gender effect in that females spent more time feeding on this fruit than males. ESFR were eaten primarily in the dry season, when females were pregnant. This was a small tree approximately 3 m tall, and was distributed in certain areas as a number of single, widely dispersed trees. Single fruits were small and were dessicated when eaten in the dry season. Since this was a monopolizable fruit, females may have fed more on this food due to female feeding priority.

GAFL was associated with a relatively higher agonistic index and gender effects, with females feeding more on this food. Within the same sex, there were no rank effects. GAFL, (9-10 m tall) was found in the drier portions of the reserve, and was distributed as single trees in this region. This was a very seasonal food item, available for approximately one week. Flower production was staggered, so that only a limited number of flowers were available on any one tree. The ringtailed lemurs frequently visited these trees, often more than once per day. Although this was a contested food, the limited availability of the flowers, and the tendency to visit the trees frequently resulted in no clear rank effects for females. This food may have been used more by pregnant females due to nutritional needs, as males had very low percentages of this food in their diet.

TIFR were associated with both a low agonistic index and no rank effects. This is a fairly common tree, especially in the portions of the reserve near the river (Sussman, 1991) They are large canopied trees ranging in height from 9 - 13 meters, and have wide canopies. Fruits of this species were eaten in the trees as well as on the ground and were one of only three species of *L. catta* foods which were large enough to be held in the hand. They could and were carried in the mouth by an individual who therefore was not tied to a particular feeding patch, and did not necessarily lose fruits when displaced.

Both TILV and MCLV were associated with lower agonistic indices and no rank effects. TILV were dispersed on large *T. indica* trees, and if individuals were displaced they could easily move to another spot. MCLV were distributed in discrete patches which could often support the entire troop. When the patch was too small, males would wait for the females to finish. Like TILV, a displaced individual could find another feeding site.

AMLV had a higher agonistic index, relative to the other two leaf species, but no rank effects. AMLV was a widely dispersed, nonindigenous spiny, weed species which was available during the latter part of the dry season, and which was located only in the dry river bed adjoining the reserve. It was also one of the few *L. catta* foods which was large enough to be held in the hand. The lemurs would dig the weed out of the river bed, turn it upside down so that the spines were pointing away from the animal's mouth, and then eat the root and stem. This was a highly contested food, as individuals would attempt to steal the large leaves from one another. However, like TIFR, the lemur was not tied to a food patch and a displaced individual could move off with the weed in its mouth and feed elsewhere. This is a case of a food item which was widely dispersed and yet was associated with a fairly high agonistic index relative to other leaves. In addition to food distribution, the value of a food is clearly important in modifying rates of agonism. AMLV had large leaves and a water-bearing root which presumably made it attractive during a season of limited food and water. In addition, the food was located out in the open river bed, in an area where raptors often roosted. The lemurs were visibly nervous when feeding on these patches (based on vigilance behaviors and tendency to leap back into the trees at the slightest disturbance) and my general observations were that not only was the food valuable, but that feeding time on it was limited as the lemurs all fed as a group, and as soon as one animal headed back for the forest the rest would follow. This is similar to results obtained in a captive study of rhesus macaques by Belzung and Anderson (1986) who offered foods of varying values (bananas only, carrots only, mixed) and distribution (clumped or dispersed). Subordinate individuals normally avoided feeding agonism from higher-ranking individuals by staying outside the feeding area when food was clumped. However, when foods were of high value (e.g. bananas) but were dispersed rather than in piles, subordinates endured greater feeding agonism by feeding next to high ranking individuals, but subordinates also attained their highest feeding scores under these conditions. High-ranking individuals had the poorest feeding scores when bananas were dispersed.

These results differ somewhat from Janson (1985b) who found a positive relationship between increased aggression and higher ingestion rates for

dominant brown capuchins. In this study high levels of aggression were not always associated with rank effects. For example, TAFR and APFR were associated with higher feeding aggression but no rank effects, indicating that the distribution of foods can mediate these two variables.

The Advantages of Rank

High rank has been related to feeding advantages in a number of species. Whitten (1983) found that although there were low levels of feeding agonism among female vervets (*Cercopithecus aethiops*), high rank was associated with greater intake of some clumped foods. This was due to the tendency for high-ranking females to monopolize such resources, and for low ranking females to avoid feeding near high-ranking females. Barton (1989) reports that among female olive baboons, high rank was associated with greater daily intakes of total dry weight, but not with the quality of foods. Janson (1985b) observed that at food sites characterized by high feeding aggression, dominants fed better than subordinates among wild brown capuchin monkeys, *Cebus apella*. Among captive rhesus monkeys, high rank was associated with greater access to feeding sites and with lower levels of feeding displacements, especially in groups receiving the least food relative to overall requirements (Deutsch and Lee, 1991). Numerous studies on wild and captive populations have reported rank advantages associated with feeding on clumped food resources (Japanese macaques: Iwamoto, 1987; rhesus macaques: Brennan and Anderson, 1988; bonnet macaques: Boccia et al., 1988; vervets: Wrangham and Waterman, 1981; baboons: Altmann and Muruthi, 1988;

If high rank is to be associated with greater reproductive success, then rank advantage should be most clearly demonstrated within a feeding context, especially for females (Wrangham, 1980). In this study, for all seasons, high rank was associated with a greater percentage of wins during direct contest competition (ie. feeding displacements) for both females and males. High rank was also associated with higher percentages of wins involving both aggressive and nonaggressive feeding agonism, and low rank was associated with more losses of both types.

High ranking females had greater yearly intake of fruit by weight, than lower-ranking troop members. Furthermore, fruit made up a higher percentage of the higher ranking female's top ten foods. For lower-ranking females, leaves made up a higher percentage of their top ten foods, and in the larger Green troop lower-ranking females had a greater intake of leaves. Thus high rank was associated with greater fruit feeding overall. One might then be tempted to argue that greater rank allowed preferential access to more "valuable" foods, but the case is not that simple. First, as has been argued in Chapter 3, fruits and leaves are not interchangeable food types, and both are important to provide a balanced diet. It is therefore difficult to attach value to different foods at this level, although future analyses of micronutrients for *L. catta* foods should help to clarify this.

Second, to even begin to associate higher rank with some ecological advantage, the advantage must come when the individual most needs it, i.e. during times of reproductive and/or dietary stress. During the wet season, when females lactated, rank effects associated with fruit feeding were modified by reproductive state. Thus in Black troop the top-ranking female did have the greatest fruit intake, but in Green troop the top-ranking female, 13, fed less on fruit, and she was nursing. It should be noted that it was not possible to statistically delineate rank effects from reproductive effects due to small samples sizes. Nevertheless, the reproductive state of the female, lactating or not, appeared to be the key influence, with lactating females feeding less on fruits and more on leaves at this time. During the dry season, when all females were pregnant, high rank was not associated with greater fruit feeding due to reduced fruit resources and to its more random distribution. However, the *cost* of foraging during the dry season was most likely greater for lower-ranking females. Lower-ranking females used more active forms of movement during foraging, and they expended more energy in agonistic feeding displacements with males who tended to be their nearest neighbors during feeding. This resulted in lower-ranking females tending to focus on less costly food sources, i.e. leaves during the dry season.

The interplay between rank and reproductive state can exacerbate the effects of resource competition, to the detriment of lower-ranking females.

Low ranking lactating females used more expensive forms of foraging (i.e. more active movement) than high-ranking lactating females. Surprisingly, low-ranking females consistently had equal or even greater feeding losses overall, as well as more aggressive feeding losses than did troop males, indicating that low-ranking females potentially face more severe feeding competition than males, regardless of female feeding priority. In addition, during the lactation (wet) season low-ranking females in general had greater feeding losses overall, and more of these losses involved aggressive displacements. Taken as a whole, the greatest costs may be accrued by low ranking lactating females, and behavioral adaptations by such individuals to mitigate these effects will be more fully explored in Chapter 6.

During the dry season low ranking females faced more potential feeding competition. They had equal or greater percentages of female nearest neighbors, and because all of them were pregnant, they would therefore have similar dietary needs. One repercussion of this was an increase in feeding losses during the dry season, which was equal or even higher than male feeding losses for some low ranking females. This carried over into the birth season where low rank again was associated with greater feeding losses. Lower-ranking females also used more expensive modes of movement, such as climbing and leaping, during foraging and other activities.

As already noted, there is evidence that male members provided lower-ranking females with more direct feeding competition at this time. During the dry season, lower-ranking females had males more often as their nearest neighbors during feeding bouts. Lower ranking females reacted to this by exhibiting a greater increase of nonaggressive feeding displacements during the dry season. More important, low ranking females responded directly to closer male feeding proximity by increasing feeding agonism directed toward males. This is unlike feeding agonism between females, which tended to be maintained at similar or lower levels in the dry season, compared to the wet season. Low ranking females responded to these pressures by using more species in the dry and birth seasons. This resulted in lower-ranking females having less dietary overlap with other females.

High-ranking females exhibited none of these behaviors. They showed a greater reduction in aggressive agonism during the dry season, most likely as a response to reduced food types associated with greater agonism, such as monopolizable fruits. They maintained or decreased all types of displacements, complete and incomplete during the dry season. They also either maintained or decreased feeding agonism directed toward males in the dry season.

Rank can also affect male feeding behavior. The tendency for central males to exhibit closer monitoring behaviors of troop females (Sauther, 1991, see also Chapter 3) is the most probable reason that these males had a diet more similar to these females, especially during the wet season which is just prior to the mating period.

Male-female dyads normally resulted in the female decidedly winning. However, some males did challenge and win during feeding and drinking bouts with younger females. This occurred only during the wet season, and only with adult-sized females who had not yet experienced their first estrus. It appears that female dominance is not inherent in this species but rather is the result of a developmental process (see also Gould, 1990) that may be finalized by a female's first estrus. As pointed out in Sauther (1991), males repeatedly approach females during the mating season to test their sexual receptivity. Nonreceptive females who fail to aggressively cuff a male away only encourage sexual advances by the male who will attempt to mount her. The same young females who were displaced several times during feeding bouts did not lose a single feeding bout to males after the mating season. Indeed, female 93 seemingly went out of her way to displace the central male (10) from feeding spots for several months after the mating season. Furthermore, all of these females (62 of Black troop; 93 and 73 of Green troop) dramatically increased the percentage of feeding displacements directed toward males (wet versus dry season: 93 and 10 = .33% versus 3%; 93 and 70 = .16% versus 1%; 93 and 50 = 1% versus 2%; 93 and 86 = 0 versus .33%; 93 and 50 = 0 versus 2%; 73 and 86 = .01% versus 8%; 73 and 30 = 0 versus 2%; 62 and 99 = 0 versus 1%; 62 and 19 = 0 versus 3%). Such consistent and large increases of feeding agonism directed toward males was not seen among older adult females (see Tables 3.12 and 3.13).

The Disadvantages of Rank

While the advantage of high rank for primates has been promoted in the literature, little attention has been paid to its potential disadvantages. Cheney et al. (1981) reported greater rates of predation on higher-ranking vervet females, and increased stress has been associated with high levels of feeding aggression among high-ranking individuals, (Chamove and Bowman, 1978) but little else has been mentioned. Among ringtailed lemurs high rank was associated with less time spent in leisure activities such as grooming. This is the opposite result as that found by van Noordwijk and van Schaik (1987) who observed that among long-tailed macaques high ranking individuals groomed more. High-ranking ringtailed lemurs were involved in more expensive forms of agonistic interactions such as aggressive feeding displacements involving chasing, biting and cuffing.

With respect to feeding behavior, high rank was also associated with lower feeding efficiency. In both troops, during the wet season, highest-ranking males and females had lower feeding efficiency ratios than did low ranking individuals, and this also held true for the top-ranking female in Black Troop during the dry season. In Green Troop the top-ranking female did better than most females during the dry season, but the highest efficiency was still exhibited by the lowest-ranking female (93).

There are at least two possible explanations for lower feeding efficiency in high-ranking individuals. First, because the highest-ranking individuals can feed without being displaced, they can afford to be more discriminating and spend more time foraging for the "best" foods. In terms of fruit feeding, "best" is most likely synonymous with "ripe" since most fruits were similar in size, and all except TIFR were small, juicy berries. This explanation has little direct support because there were no rank effects associated with percentage of ripe fruits taken. Similarly there is no support for this explanation if "best" means young leaves because most leaves eaten were either from young herbaceous species, or deciduous species all of which tended to be young buds or leaf flush at the same time (see above). In

addition there was no evidence of rank effects associated with the ingestion of young leaves or leaf buds.

A more feasible explanation is related to the distribution of the resources. When a resource is clumped, but no alternative source is available (i.e. single *Grewia* or QUFL trees), and when the resource is limited and can be depleted, then high rank individuals do have greater intake of this monopolizable food. However, the other individuals do not simply queue up to wait for a turn at this limited resource. All troop members actively try to enter such a tree and the high-ranking female must divide up her time between spending considerable energy displacing invading troop members, and foraging for and eating the limited ripe fruits. As one individual is chased within such a tree by the top-ranking female, others can enter and feed until they too are displaced. The end result is that some lower-ranking individuals are actually more efficient at feeding on this type of food.

However, when foods are clumped in space, but more than one of the resource are available (i.e. groves of TAFR and APFR) high rank clearly has an advantage in terms of feeding efficiency. High-ranking individuals are able to forage and feed, with less time spent on displacing others since troop members can spread out among such resources. In these cases high ranking individuals do not have greater intake of these foods because they are not able to monopolize the resource.

In cases where food is spread out, but any single tree is small enough to be monopolizable (i.e. SAFR), high-ranking individuals can acquire greater intake at a higher feeding efficiency. Because of their high rank they are not displaced from the food source, and because there are other food trees, they are not losing efficiency by displacing as many individuals who can and do feed elsewhere.

Feeding costs must therefore be considered when making correlations between high rank and feeding advantages. For example, Nakagawa (1990) found for Japanese macaques that although high-ranking individuals tended to feed in higher quality patches of *Zelkova serrata* seeds, these patches were also associated with greater feeding agonism as more individuals were

attracted to the patch. Low ranking individuals tended to feed in lower quality patches of these seeds where fewer individuals fed, and thus may have encountered less feeding agonism. Nakagawa reasons that the agonistic costs associated with high quality patches may thus cancel out any advantages associated with greater intake. Greater aggression among Japanese macaques (Ihobe 1989) and rhesus macaques (Brennan and Anderson, 1988) has also been noted in association with a clumped resource. Similarly, Barton (1988) found that clumped foods were associated with greater numbers of nearest neighbors and higher rates of feeding agonism (supplants).

For ringtailed lemurs, although it is difficult to attach gross levels of nutritional value to different food types, in terms of availability ripe fruits can be seen as more valuable in that they are a more limited resource than leaves. In addition, fruits are often located on trees which can only support a certain number of individuals, i.e. are clumped in space. It has been argued above, and shown in other studies that limited fruit resources located on single small trees are associated with high rank advantages for various measures of feeding success due to the greater ability of an individual to monopolize or limit feeding access of others. For ringtailed lemurs, these food patches (such as 03FR and G6FR) are also associated with greater feeding costs. Rates of feeding displacements are much higher (see Table 3.20, Chapter 3) as are the agonistic indices (Table 4.22). These costs not only impact low-ranking females, but also high-ranking females in terms of energy expended in attempting to maintain sole access to such feeding patches, and in lower feeding efficiency. As Plimpton et al. (1981) have noted for an experimental test in which raisins were either scattered on top of a gravel pile, or placed underneath "In situations where food resources are limited and relatively difficult to obtain (as in the buried condition) animals are under pressure to obtain food while monitoring the behavior of others which also seek access to the foraging sites" p 183.

Hence the feeding behavior of high-ranking individuals may be viewed as a trade-off between greater food intake and feeding efficiency. Higher intake of a single, monopolizable food resource will be at the expense of greater energy expenditure (via feeding agonism) and lower feeding efficiency. Lower intake of more numerous clumped resources has the advantage of

reduced feeding costs. Thus greater rank per se is no guarantee of greater food intake. Only in situations where a higher ranked individual can directly limit other member's food or water intake (i.e. clumped, single, monopolizable resource which can be depleted, i.e. is limited) is there a rank advantage. Again, the distribution and availability of resources greatly influences the expression of high rank advantage.

CHAPTER 5

INTERGROUP CONTEST COMPETITION AND SOCIAL SIZE EFFECTS IN RINGTAILED LEMURS

INTRODUCTION

Models which seek to address the costs and benefits of social group-living all posit resource competition as one disadvantage of social living (Alexander, 1974, Van Schaik and Van Hoof, 1983; Van Schaik, 1983; Terborgh and Janson, 1986; Wrangham, 1980). Such models differ in the importance of inter versus intra-group competition, and on what factors encourage individuals to tolerate living in larger groups. "Predation" models (Alexander, 1974; Van Schaik and Van Hoof, 1983, Van Schaik, 1983; Terborgh and Janson, 1986) all focus on intragroup feeding competition as the ultimate cost for group living, which intensifies as group size increases. For such models, increased predator detection is the driving force behind larger groups, and group size is seen as fluctuating as a response to these two factors. "Resource defense" models acknowledge intragroup competition, but argue that the advantages gained by individuals (specifically females) joining together to defend resources surpasses the feeding costs within a group (Wrangham, 1980). In this model successful resource defense is the ultimate pay-off for group living. Variations of this model include the addition of male resource competition (Dittus, 1986) and greater emphasis on the distribution and availability of resources in altering sub-group size (Rodman, 1988) and in affecting inter and intra-group competition (Isbell, et al. 1991).

These two models have been applied to free-ranging primate species with varying results. Some studies report support for the predation model. Among free-ranging yellow baboons, no marked difference in foraging efficiency ratios have been found for small versus large groups, but smaller groups did spend more time near trees (presumably for predator escape), and

were more likely to rest on elevated perches which may have increased their ability to detect predators (Stacey, 1986). Larger groups of long-tailed macaques detected nonhabituated human observers at greater distances than smaller groups, supporting the contention that larger groups are better at predation detection (van Schaik et al., 1983). Group size among long-tailed macaques may also vary based on the presence or absence of large felids. On the island of Simeulue, which has no large felids, group sizes were smaller than among Sumatran populations of long-tailed macaques where tigers and golden cats were present (van Schaik and Van Noordwijk, 1985). However, group sizes of long-tailed macaques of Borneo are similar to Sumatra, and yet Borneo has no tigers or golden cats (Rodman, 1988). Variance in mortality among long-tailed macaques (which has been assumed due to predation) rather than birth rates (access to food) has been posited as determining female reproductive success (van Noordwijk and van Schaik, 1987). Low-ranking and older females, who left the main party to forage in subgroups when fruit resources became too small to accommodate all individuals, had higher mortality rates. Again they assumed this was due to predation (van Noordwijk and van Schaik, 1985).

Higher rates of aggressive food competition within groups versus between groups has been reported for brown capuchin monkeys (*Cebus apella*) (Janson, 1985b). Groups only fought over access to fig trees, and even this was rare. The effects of group size on anti-predator and foraging behaviors for wedge-capped capuchin monkeys has also been studied (de Ruiter, 1986). Smaller groups were characterized by spending more time foraging, scanning (presumably for predators), less grooming and less agonism (although not significantly) and by having greater travel distances. Group size had no effects on diet in the wet season, but during the dry season there were marked variability, with the larger group using more animal sources and less fruits than the smaller groups. De Ruiter noted that more foraging in the smaller group is the opposite of what might be expected if smaller groups are associated with less feeding competition.

Slightly different results have been reported for long-tailed macaques. In one study (van Schaik, et al. 1983), larger groups were associated with more

travel, and agonism, which is similar to de Ruiter's (1986) results. However, larger groups were characterized by less grooming and foraging, which is the opposite of that found for the wedge-capped capuchins studied by de Ruiter.

Other studies indicate the limitation of the predation models and highlight the importance of group defense. One of the most dramatic consequences of a troop's inability to defend resources from others occurred when one troop of toque macaques took over another troop's range and fused with them (Dittus, 1986, 1987). Within 8 years of the takeover all of the members of the subjugated group, with the exception of one offspring, died. This was most likely due to the fact that the invading troop maintained its priority of access to resources even after fusion. This occurred in spite of the fact that after fusion the group size was more representative of median population sizes, and this presumably increased predator detection. Thus larger group size, per se was not mediated by predator pressure alone (Dittus, 1986).

Frequent intergroup encounters among different groups of patas monkeys have been reported, with females and immatures being more involved than adult males when intergroup encounters were over particular resources (Chism, et al., 1984).

Mixed species of *Saguinus mystax* and *S. fuscicollis* exhibit little intragroup feeding competition due to species differences in body size, foraging behavior and diet. However larger mixed species do have greater success in maintaining access to important food resources (Garber, 1988).

Vervet groups with overlapping ranges have been observed competing with other groups (Whitten, 1984). Both sexes participated in intergroup encounters. Groups had better success in defending areas that they visited frequently. Group size had an effect as well. Smaller sub-groups of lower-ranking females were unable to successfully defend resources from larger groups, even when such groups were displaced when encountering the sub-group's original troop. There was little support that sub-group size negatively affected feeding or locomotor costs (Whitten, 1988). Instead, larger

sub-groups were associated with feeding advantages, such as greater net energy per feeding bout. Among vervet monkeys with established ranges, larger groups had bigger and higher quality ranges, and were more likely to enter the ranges of smaller groups, with the smallest groups suffering the least predation (Cheney and Seyfarth, 1987). Larger groups were more successful than smaller groups in moving into new areas and acquiring more food trees, with most smaller groups being pushed into unfamiliar areas associated with greater rates of predation (Isbell et al., 1990).

Group size effects on female and male reproductive success in wedge-capped capuchin monkeys have also been studied (Robinson, 1988). Based on demographic life tables collected over a 10 year period it was found that both female and breeding male reproductive success was greater in larger groups. Greater female reproductive success in larger groups was most likely a consequence of the ability of larger groups to displace smaller groups at monopolizable fruit sources. However, unlike Wrangham's model, Robinson argues that larger group dominance was tied to greater numbers of males in larger groups who are responsible for more of the direct intergroup fighting.

These varying results indicate the need for more specific quantitative analyses to determine the relationship between group size, intergroup defense, predator pressure, and foraging behaviors, including feeding competition. In this chapter the effect of these various ecological factors on foraging behavior is studied for two different-sized troops of *Lemur catta*.

RESULTS

Two troops were compared for group size effects. Green troop had 14 members (ten adults, 2 juveniles and 2 infants). Black troop was smaller, with 9 members, (6 adults, 1 juveniles and 2 infants). Since different reproductive states alter feeding behavior (Chapter 3) if the two troops differed greatly in their makeup this could confound the results. However the two troops were quite similar in breakdown of animals at particular reproductive states (Green troop: wet season, 2 lactating females, one high ranking, one low ranking, 3 nonlactating females, 1 high ranking, 2 low

ranking, 5 males; dry season, 5 pregnant females, 5 males; Black troop: wet season, 2 lactating females, one high ranking, one low ranking; 2 nonlactating females, one high ranking, one low ranking, 2 males; dry season, 4 pregnant females, 2 males). Thus the troops differed mainly in the number of males. Group ranges for all troops vary depending on location and season, but overlap of ranges is high, with little or no areas of exclusive use (Sussman, 1991).

GROUP SIZE AND RESOURCE COMPETITION

It might be expected that larger troops create greater potential feeding competition, because individuals are required to feed more closely to one another. Conversely, larger troop size may result in individuals feeding further from one another in an attempt to avoid increased feeding pressure. To test for this, the mean proportion of nearest neighbors by identical food type and distance were compared (Table 5.1). These are only cases where nearest neighbors fed or foraged on the same food item. Thus this represents a measure of group spread while feeding on certain foods. There was no clear relationship between group size and nearest neighbor distances. For some foods (QUFL, ESFR) nearest neighbors fed closer to one another in the larger Green troop, but for other resources (APFR, TIFR-wet season, TILB) neighbors fed closer in the smaller, Black troop. Overall, the two troops were strikingly similar in mean distances of nearest neighbors when feeding on the same foods.

Table 5.1. Mean Proportion of Nearest Neighbors by Distance and Food for Black and Green Troop.

BLACK TROOP				GREEN TROOP			
Food	<1-3m	3-6m	6->9m	Food	<1-3m	3-6m	6->9m
APFR ¹	.79	.05	.16	APFR ¹	.67	0	.33
GRFR ²	0	0	0	GRFR ²	0	0	0
TIFR ³	.80	.06	.14	TIFR ³	.51	.17	.32
TIFR ⁴	.53	.35	.12	TIFR ⁴	.58	.14	.28
MCLV	.90	0	.10	MCLV	.93	0	.07
TAFR	.87	.13	0	TAFR	.80	.09	.11
TILB	.78	.16	.06	TILB	.68	.28	.04
ESFR	.38	.24	.38	ESFR	.60	.20	.20
QUFL	.86	.08	.06	QUFL	.93	.03	.04
GAFL	1.00	0	0	GAFL	1.00	0	0
SAFR	.83	.03	.14	SAFR	.75	.14	.11
$\bar{x}$	.70	.10	.11	$\bar{x}$	.68	.10	.14

1 See Table 2.4 for the complete Genus and species of each plant food.

2 All *grewia* fruits were combined as they did not differ in phenology or distribution.

4 Wet Season.

3 Dry Season.

The assumption of greater feeding competition in larger groups was assessed by comparing yearly food weights ingested for the top 20 foods (Table 5.2). Individuals of the larger troop, Green, had greater mean intake of nonTIFR fruits, but the smaller troop, Black, fed more on TIFR. Neither flower nor leaf feeding varied, markedly, between troops. Total mean intake (not including TIFR) was greater in the larger troop, but if TIFR is included

the smaller troop had the higher mean intake, but the differences were not significant.

Table 5.2. Mean weights (in grams) of the top 20 foods eaten by Black and Green troop for the year.

TROOP	*FRUITS	LEAVES	FLOWERS	TIFR	TOTAL No TIFR	TOTAL With TIFR
BLACK	1.79	2.45	.41	42.62	4.65	46.26
GREEN	3.03	3.10	.38	25.79	6.48	32.71
DF = 14	t = 2.78 p < .004	t = .92 N.S.	t = .78 N.S.	t = 1.86 p < .04	t = 2.78 p < .004	t = 1.68 N.S.

*Does not include TIFR.

The smaller troop's greater dependence on the fruit of *Tamararindus indica* (TIFR) is most likely the result of greater availability of this fruit source within its home range (see Table 5.3) which was determined by the percentage of these species which made up the total phenological samples (see Chapter 2). However, there is no strong evidence to suggest that greater intake of nonTIFR fruits in the larger troop was simply due to the greater availability of nonTIFR fruits within their home range. Indeed, while some nonTIFR fruits were more available in Black troop's home range (ESFR, APFR) others were more plentiful in Green troop's home range (TAFR, GRFR). Furthermore, it cannot be said that Black troop's greater use of TIFR made their diet qualitatively better than the larger Green troop as there are greater potential costs associated with processing TIFR. Unlike the small juicy berries (TAFR, GRFR, APFR, ESFR-wet season), TIFR has a hard outer shell which must be cracked and discarded, and the fruits themselves are fibrous and more difficult to process. In addition, TIFR has tannins which may retard the absorption of iron, protein and minerals (Spelman et al, 1989). Future analyses of these foods should help determine this.

Table 5.3. Availability of certain tree species in Black and Green troop's home ranges.

SPECIES	GREEN TROOP	BLACK TROOP
<i>Tamarindus indica</i>	28%	52%
<i>Quisiamanthe papionae</i>	4%	10%
<i>Grewia sp.</i>	39%	19%
<i>Talinella dolphinensis</i>	21%	5%
<i>Salvadora augustifolia</i>	18%	9%
<i>Enterospermum pruinatum</i>	4%	19%
<i>Gyrocarpus americanus</i>	4%	5%
<i>Antidesma petiolare</i>	4%	19%

Table 5.4 compares mean weights ingested, per individual, by season. The smaller, Black troop had greater TIFR intake during the wet season. During the wet and transitional seasons, individuals of the larger, Green troop, had substantially greater intake of nonTIFR fruits than did individuals of the smaller, Black troop. During the dry season, the larger, Green troop had significantly greater intake of leaves.

Table 5.4. Mean weights (In grams) of the top 20 foods eaten by Black and Green troop by season.

WET SEASON

TROOP	FRUITS WITHOUT TIFRUIT	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFRUIT	TOTAL
BLACK	.89	28.49	29.38	1.27	0	2.46	30.65
GREEN	1.63	14.20	15.83	1.30	0	2.93	17.13
DF = 14	t = 4.09 p < .0001	t = 1.96 p < .03	t = 1.83 p < .05	t = .46 N.S.	t = 0 N.S.	t = .48 N.S.	t = 1.94 p < .05

DRY SEASON

TROOP	FRUITS WITHOUT TIFRUIT	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFRUIT	TOTAL
BLACK	.21	9.54	9.75	.23	.61	1.05	10.59
GREEN	.30	10.19	10.49	.73	.48	1.51	11.70
DF = 14	t = .60 N.S.	t = .28 N.S.	t = .13 N.S.	t = 4.08 p < .0001	t = .75 N.S.	t = 1.71 N.S.	t = .26 N.S.

TRANSITIONAL SEASON

TROOP	FRUITS WITHOUT TIFRUIT	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFRUIT	TOTAL
BLACK	.27	.39	.66	.16	0	.43	.82
GREEN	.65	.40	1.05	.15	0	.80	1.20
DF = 14	t = 3.85 p < .002	t = .00008 N.S.	t = 1.34 N.S.	t = .10 N.S.	t = 0 N.S.	t = 3.61 p < .0001	t = 1.11 N.S.

Food weights ingested by troop members for identical species and parts is shown in Table 5.5. Overall, there were no marked differences between troops for mean food weights ingested. Intake of specific foods did differ, by troop, but there was no indication that this was related to troop size. Again, the variability was more likely due to the availability of each food type within a troop's normal home range (Table 5.3). For all tree species, except QUFL, the troop which had a higher intake of a particular tree species also had a greater percentage of this species within its home range. For example, Green troop had greater intake of 03FR (*Grewia sp.*) and also had more of these trees within its home range (39% versus only 19% for Black troop).

Feeding efficiency did not differ markedly between troops (Table 5.6)

Table 5.5 Comparison of mean food weights ingested for identical species and parts in Black and Green troop.

FOOD	BLACK TROOP	GREEN TROOP	RESULTS
03FR	.004	.02	DF = 14, t = 2.67, p < .004
QUFL	.04	.06	DF = 14, t = 2.56, p < .01
SAFR	.04	.09	DF = 14, t = 4.18, p < .0001
TILB	.02	.01	DF = 14, t = 2.97, p < .01
MCLV	.008	.02	DF = 14, t = 1.34, p = .12
TALV	.009	.03	DF = 14, t = 2.54, p < .006
ESFR	.06	.01	DF = 14, t = 3.65, p < .002
APFR	.04	.004	DF = 14, t = 2.16, p < .03
$\bar{x}$	.03	.03	DF = 14, t = .61, p = .26

Table 5.6. Mean feeding efficiency ratio for Green and Black Troop by season.

TROOP	Wet	Dry
BLACK	2.13	.58
GREEN	1.65	.78
	t = .63 N.S.	t = .76 N.S.

*Ratio of 1 = equal time spent feeding and foraging. The higher the ratio, the more time spent feeding relative to foraging.

Greater competition associated with larger group size should result in higher levels of agonism. Agonism by context is shown in Table 5.7. Troop size had no effect for most of these measures. Only agonism over drinking spots at tree hollows showed marked difference, with the larger, Green troop exhibiting more agonism.

Table 5.7. Agonism by context for Green Troop and Black Troop.

	Feed	Forage	Stink-Fight	Lick Killy	Rest	Space	Drink	Groom
BLACK	.78	5.91	1.18	7.08	3.58	2.00	.50	2.08
GREEN	.78	1.25	1.27	11.00	2.06	3.00	2.41	.73
	t = .13, N.S.	t = 1.32, N.S.	t = .07, N.S.	t = .90, N.S.	t = .63, N.S.	t = .12, N.S.	t = 1.82, p < .05	t = .83, N.S.

Focusing on feeding agonism by food part, it can be seen from Table 5.8 that there were no group size effects for aggressive feeding agonism (i.e. those involving chases, lunges, cuffing and biting). For nonaggressive feeding agonism (i.e. approach-retreat) there were several meaningful differences between troops. Black troop had more nonaggressive feeding agonism over fruit than did Green troop, and Green troop had greater percentages of nonaggressive feeding agonism over leaves. Total agonism did not differ markedly by group size (Table 5.9).

Table 5.8. Comparison of the mean percentage of aggressive and non-aggressive agonism for food types in Black and Green Troop.

AGGRESSIVE

FOOD TYPE	BLACK TROOP	GREEN TROOP	
FRUIT	26%	34%	$t = 1.08, n.s.*$
LEAVES	7%	13%	$t = .82, n.s.$
FLOWERS	2%	2%	$t = .03, n.s.$

NON-AGGRESSIVE

FOOD TYPE	BLACK TROOP	GREEN TROOP	
FRUIT	31%	17%	$t = 1.69, p < .06$
LEAVES	3%	8%	$t = .82, p < .004$
FLOWERS	2%	5%	$t = .48, n.s.$

*DF = 22

Table 5.9. Comparison of the mean percentage of agonism by food type in Black and Green Troop.

Food Type	Black Troop	Green Troop	Significance
Fruit	29%	26%	$t = .45, N.S.*$
Leaves	5%	11%	$t = 1.50, N.S.*$
Flowers	4%	2%	$t = .91, N.S.*$

*DF = 22

Comparing feeding agonism by identical foods (Table 5.10) indicates that overall there were no group size effects for feeding agonism over the same foods. Some foods were associated with great agonism in the larger, Green troop, and others in the smaller, Black, troop. Again this is related to

availability. When there were differences, higher percentages of agonism occurred for the troop which had more of such foods within their range. The only two exceptions are SAFR and TIFR. Black troop had very high levels of feeding agonism over SAFR. This fruit species was available for only a short period and Black troop had to travel a considerable distance to reach this resource. SAFR used by Black troop was deep in the home range of another troop (Yellow troop) which made Black troop visibly nervous (troop members easily startled, more scanning of the area) and at the end of each feeding bout the troop would race back to their own home range. Indeed on several occasions Yellow troop chased Black troop from the area. It is thus likely that individuals tended to feed more closely to one another under these circumstances, and hence incurred higher levels of feeding agonism. This is supported by Table 5.10 in that Black troop had more near neighbors while feeding on SAFR than did Green troop, who did have SAFR within its range. It is not immediately clear why the larger, Green troop had greater agonism over TIFR as this was less available in their home range.

Table 5.10. Percentage of Agonism Over the Same Foods for Black and Green Troop.

LEAVES		FRUITS		FLOWERS	
Black Troop	Green Troop	Black Troop	Green Troop	Black Troop	Green Troop
ACLF = .14	ACLF = .04	BEFR = .22	BEFR = .02	GAFL = .04	GAFL = .08
MCLF = .01	MCLF = .06	ESFR = .14	ESFR = .05	MFFB = .03	MFFB = .15
PELV = .03	PELF = .01	GRFR* = .18	GRFR = .36	QUFL = .13	QUFL = .26
TILB = .08	TILB = .04	TAFR = .46	TAFR = .55	SAFB = .03	SAFB = .04
4FLF = .03	4FLF = .03	TIFR = .09	TIFR = .20		
H1LF = .09	H1LF = .19	CLFR = .04	CLFR = .03		
8CLF = .04	8CLF = .01	SAFR = .66	SAFR = .29		
$\bar{X} = .06$	$\bar{X} = .05$	$\bar{X} = .23$	$\bar{X} = .21$	$\bar{X} = .06$	$\bar{X} = .13$
Black versus Green $t = .20$, N.S.		Black versus Green $t = .12$, N.S.		Black versus Green $t = .138$, N.S.	

* All *Grewia* species were combined as they were similar in structure, phenology and distribution.

Feeding agonism where one individual steals food from another might indicate levels of feeding competition and were compared by troop. Black troop had a mean yearly percentage of food stealing of 8.08 whereas Green troop had a mean of only 2.25 ($t = 1.54$, $p < .04$). Markedly higher rates in the smaller Black troop are most likely due to the greater availability of TIFR within their home range, as the fruit of *Tamarindus indica* were one of the few ringtailed lemur foods which could be held in the hand and thus stolen outright.

To determine the relationship between various ecological factors and feeding agonism, correlations were produced and are listed in Table 5.11. Feeding agonism was only significantly correlated with intergroup encounters, and this occurred only in the larger Green troop.

Table 5.11. Correlation coefficients for feeding agonism.**GREEN TROOP**

Variable	Feeding Agonism
Leaf Feeding	-0.05
Flower Feeding	+0.27
Fruit Feeding	-0.17
Inter-troop Encounters	+0.59*
Predators Encountered	+0.04
Leaf Availability	+0.30
Flower Availability	+0.14
Fruit Availability	+0.33

* $p < .04$ **BLACK TROOP**

Variable	Feeding Agonism
Leaf Feeding	-0.07
Flower Feeding	+0.03
Fruit Feeding	-0.11
Inter-troop Encounters	+0.17
Predators Encountered	+0.11
Leaf Availability	+0.08
Flower Availability	-0.09
Fruit Availability	+0.02

While group size had no negative effects on food intake or feeding agonism, larger groups might have to expend more energy in foraging activities. As already noted (Table 5.7) there were no significant troop size effects for time spent foraging, although the smaller troop actually spent more time foraging. However, another measure of foraging is the percentage of travel. Travel denotes movement of the whole troop from one food patch or feeding area to another and is differentiated from movement within any feeding area (Sussman, 1972). The mean proportion of time spent travelling is compared in Table 5.12. There were no differences in the wet and dry season. However, Black troop, the smaller group, had markedly more travel during the transitional season. This is due to the fact that Black troop focused on SAFR which was available during this period. Black troop did not have SAFR within its normal home range and had to travel an average of 4-5 ha to reach SAFR which was found only in the drier portions of the reserve.

Table 5.12. Mean proportion of time spent travelling by Black and Green troop by season.

TROOP	Wet	Dry	Transitional
BLACK	4.24	3.54	7.16
GREEN	4.58	3.30	2.57
DF = 14	t = .43 N.S.	t = .25 N.S.	t = 2.08 p < .02

The larger, Green troop, did have a greater proportion of both active movement and walking during the wet season, and they had a greater movement ratio (i.e. they spent markedly more time in active versus walking movement) in the dry season than the smaller, Black troop (Table 5.13).

Table 5.13. Mean proportion of time spent in active movement (climp, leap, hop, run) and walking, and movement ratio for Black and Green troop by season.

	ACTIVE		WALK		*RATIO	
TROOP	Wet	Dry	Wet	Dry	Wet	Dry
BLACK	.29	.29	.71	.69	.46	.49
GREEN	.37	.35	.63	.64	.60	.61
	t = 1.78 p < .05	t = 1.26 N.S.	t = 1.78 p < .05	t = .63 N.S.	t = 1.32 N.S.	t = 1.45 p < .05

*Ratio of 1 = equal time spent in active movement and walking.
The higher the ratio, the more active movement utilized.

SPATIAL RELATIONSHIPS

Predation Pressure Versus Resource Availability

Throughout the year all occurrences of troop encounters with potential predators (primarily raptors) were recorded (Sauther 1989). Although it can be argued that the presence of an observer may reduce overall encounters, the *pattern* of encounters should not change. These patterns provide a more realistic measure of predation pressure as predation is so rarely observed in wild populations. It should also be noted that previous assumptions that Madagascan lemurs are more immune to predation due to the absence of large felids (van Schaik and van Hoof, 1983) ignores the impact of important carnivores such as the fossa (*Cyrtoprocta ferox*), and aerial raptors which are known predators of young lemurs (Ratsirarson, 1985). Previous researchers have noted the importance of predation pressure on lemur behavior (Jolly, 1966; Sussman, 1972, Richard, 1978). Furthermore, Langrand and Goodman have found evidence of substantial mouse lemur predation by owls (pers. comm.). There is thus no evidence suggesting lemurs are under relaxed predation pressure. Thus if predation plays an important role in affecting group size or social relationships within and between groups, its impact should be measurable in populations of ringtailed lemurs.

It might be expected that predator pressure should be negatively correlated with time spent alone, i.e. as more predators are encountered, solitary activities should decrease. Correlations, presented in Table 5.14 showed no such relationship. In both troops resource availability was best correlated with solitary activities. The availability of leaves was positively correlated with time spent alone. In the larger, Green troop, solitary activities were also correlated with both fruit availability and fruit feeding.

Factors influencing close interindividual distances (<1-4m) varied between troops. In the larger, Green troop important factors were again resource dependent, with flower feeding being positively correlated, and fruit feeding being negatively correlated with close nearest neighbor distances. In the smaller, Black troop fruit weights but not flower availability was significantly correlated with close interindividual distances. Predator pressure had no effect on close neighbors in the larger Green troop. However, in Black troop predator pressure was positively correlated with near neighbors, although this did not quite reach significance ($p = .09$).

Intergroup Encounters

Intergroup encounters of ringtailed lemurs have been described for populations living at Berenty (Jolly, 1966, Sussman, 1972; Jolly, 1972; Jones, 1983; Koyama, 1991). During the year all occurrences of intergroup encounters between neighboring troops at Beza Mahafaly ($n = 71$) were noted and are presented in Figure 5.1. Such encounters primarily involved female members who would aggressively defend or attempt to acquire access to food trees. These interactions could become quite violent. Females physically fought with one another, and on several occasions females were knocked out of trees. In one observed case the top-ranking female of Green troop fell 6-7 meters with her infant on her back during a fight with a female from another troop.

Table 5.14. Correlation coefficients for solitary activities and close feeding.

GREEN TROOP

Variable	Solitary Activities (> 8m)	Close Feeding (< 1- 4 m)
Leaf Availability	+.60*	-.41
Flower Availability	-.42	+.62**
Fruit Availability	+.59*	-.37
Leaf Feeding	+0.37	+.41
Flower Feeding	-0.41	+.53
Fruit Feeding	+0.58*	-.54***
Predators Encountered	+0.08	+.02

*p < .04, n = 10

**p < .03, n = 10

***p < .05, n = 10

BLACK TROOP

Variable	Solitary Activities (> 8m)	Close Feeding (< 1- 4 m)
Leaf Availability	+.65**	-.54
Flower Availability	+.07	+.26
Fruit Availability	+.27	-.13
Leaf Feeding	+0.32	+.25
Flower Feeding	-0.08	+.38
Fruit Feeding	+0.16	-.63*
Predators Encountered	-0.23	+.51

*p < .03, n = 6

**p < .02, n = 6

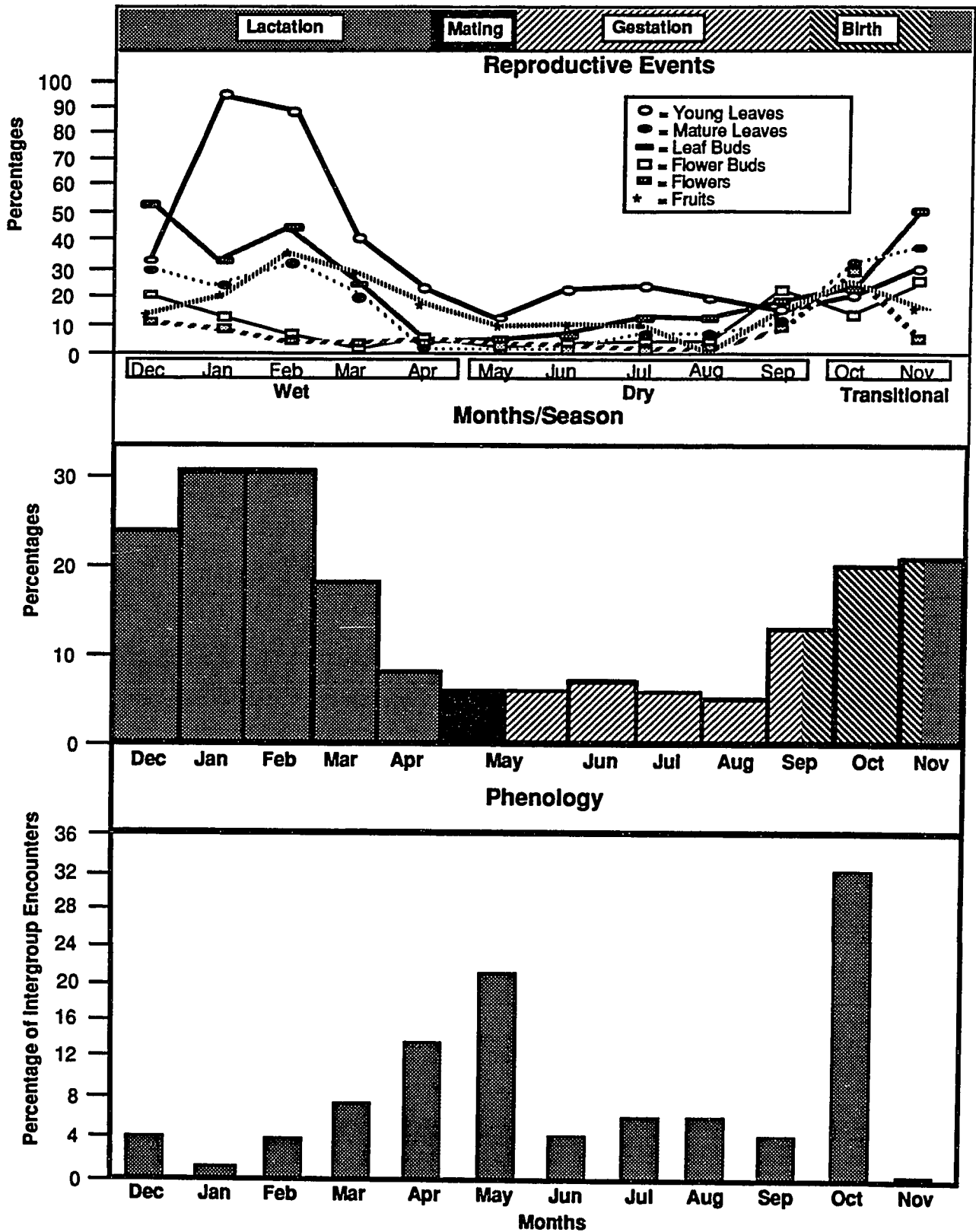


Figure 5.1 Intergroup Encounters Between Troops of Ringtailed Lemurs Relative to the Phenological Availability of Food at Beza Mahafaly, 1987-1988.

Of these encounters, over half (54%) were related to a clearly identified resource such as flower or fruit trees, or water sources. In all of these cases the winning troop remained and used the resource. Two clear peaks in these encounters occurred. The first was March-May which coincided with both a gradual reduction in overall food availability, and the weaning period for infant *L. catta*. The second peak was in October when foods were still relatively scarce and which coincides with birth and early lactation (see Fig. 5.1).

Although all females participated in aggressive intergroup encounters, a correlation coefficient was generated to determine if higher-ranking individuals tended to be more involved in such encounters. There was no tendency for high ranking females to participate in more of such encounters ($n = 9$; $r = +.32$, $p = .77$). In fact, based on individual percentages of involvement, in both troops it was a low ranking female who had equal or higher percentage of participation in intergroup encounters as higher ranking females (Green troop: 73 = 30%, 93 = 15%, versus 13 = 15%, 33 = 12%, 53 = 8%; Black troop: 62 = 36% versus 02 = 11%, 82 = 28%, 42 = 14%). While not reaching significance due to small sample sizes, among males higher-ranking individuals were more involved ($n = 7$; $r = .62$, $p < .13$).

To determine what sort of relationship existed between various ecological factors and intergroup encounters, correlation coefficients were produced and are listed in Table 5.15. Overall, the availability of fruits (both troops) and fruit feeding (Black troop) were significantly correlated with intergroup encounters. As fruits became more available, the incidence of intergroup encounters increased as well. Flower feeding was also positively correlated with intergroup encounters, but this only reached significance in the smaller Black troop.

Breaking down these factors by season, Table 5.16 indicates that during the wet season, as food became less available intergroup encounters involving the larger Green troop increased. The same direction is seen for Black troop, but did not reach significance.

Table 5.15. Correlation coefficients for inter-group encounters.**GREEN TROOP**

Variable	Inter-group Encounters
Leaf Feeding	+0.13
Flower Feeding	+0.43
Fruit Feeding	-0.44
Predators Encountered	+0.03
Availability of Leaves	-0.31
Availability of Flowers	+0.41
Availability of Fruits	0.76*

*p < .004, n = 10

BLACK TROOP

Variable	Inter-group Encounters
Leaf Feeding	-0.21
Flower Feeding	+0.77*
Fruit Feeding	0.60**
Predators Encountered	+0.44
Availability of Leaves	0.05
Availability of Flowers	0.18
Availability of Fruits	+0.71***

* p < .003, n = 6

* p < .03, n = 6

* p < .01, n = 6

Table 5.16 Correlation coefficients for inter-group encounters broken down by season.

GREEN TROOP		BLACK TROOP	
Variable		Variable	
WET SEASON	Inter-group Encounters	WET SEASON	Inter-group Encounters
Leaf Feeding	+0.34	Leaf Feeding	-0.27
Flower Feeding	+0.01	Flower Feeding	+.31
Fruit Feeding	-0.25	Fruit Feeding	-0.03
Leaf Availability	-0.82*	Leaf Availability	-0.39
Flower Availability	-0.62**	Flower Availability	-0.49
Fruit Availability	-0.64**	Fruit Availability	-0.18
DRY SEASON		DRY SEASON	
Leaf Feeding	-0.19	Leaf Feeding	-0.26
Flower Feeding	+0.83*	Flower Feeding	+.92*
Fruit Feeding	-0.89***	Fruit Feeding	-0.80**
Leaf Availability	-.46	Leaf Availability	-.57
Flower Availability	+.72**	Flower Availability	+.96***
Fruit Availability	+.11	Fruit Availability	+0.64****

*p < .03, n = 10

**p < .05, n = 10

***p < .01, n = 10

*p < .03, n = 6

**p < .01, n = 6

***p < .004, n = 6

****p < .05, n = 6

During the dry season, a period of reduced food availability, peaks in flower and fruit availability were correlated with noticeable increases in intergroup encounters.

DISCUSSION

FEMALE SOCIAL RELATIONSHIPS

Two competing hypotheses have been proposed to explain female relationships within and between primate groups. Van Schaik (1989) provides a model in which variance in predation pressure produce varying hierarchical systems. High predation pressure results in females forming cohesive groups as a predator defense tactic, but due to increased feeding competition this results in well-defined dominance hierarchies. Low predation pressure creates less cohesive groups and reduces intragroup competition which leads to less defined or even egalitarian social relationships within groups, and aggressive behaviors between groups.

Wrangham's (1980) model focuses on the distribution of resources as key in defining female social relationships. In his model when important resources are clumped, females will form groups to defend these areas from other groups. When the clumped resources vary in quality, dominance hierarchies within groups will form. More recently, Isbell (1991) has expanded on this model. When foods limit reproductive success, then females should always be aggressive towards other groups of females, as they can reduce food abundance (scramble competition). Unlike Wrangham's model, in her model food distribution only mediates intragroup resource competition (contest competition).

In this chapter I compared two different sized groups of ringtailed lemurs to explore how group size affected resource competition. In addition, intertroop competition was documented, and important variables affecting the patterning of such competition were presented.

GROUP SIZE EFFECTS AND INTERGROUP RESOURCE DEFENSE

Although Terborgh and Janson (1986) have predicted that "feeding competition should be greater in large groups of a given species than in small groups in the same study area" p. 214, results presented here indicate the relationship is far more complex. As in intragroup resource competition (Chapter 4) the critical variable which mediates competition is the characteristics of the resources themselves. Hence, when different-sized groups fed on the same foods, nearest neighbor distances were not significantly different for most foods. Furthermore, there were no troop size effects for identical food species. Instead, the distribution of foods played the most important role in affecting intake of specific foods, with troops feeding more on species which were more available within their normal home range.

In addition, total mean agonism over the same foods was not significantly different, and where there were troop differences, this was related to availability rather than greater competitive pressure in the larger group. It is especially important to note that the larger troop did not exhibit greater feeding agonism overall, greater proportions of food stealing, nor was it characterized by greater aggressive forms of agonism by food part, which might be expected if larger troops were accompanied by increased feeding competition. This does not mean that higher levels of competition do not occur in larger groups. Rather, the expression of such competition may be mitigated by two factors, the distribution of the resources, and resource defense. The effect of resource distribution on the degree of feeding agonism has already been discussed in the previous chapter. Suffice to say, when feeding agonism for monopolizable resources is compared, the larger troop did in fact have measurably greater agonism (see Table 5.10, GRFR: Green troop = .36; Black troop = .18, $< .05$; and Table 5.7, drinking at tree hollows: Green troop = 2.41; Black troop = .50 $p < .05$). Although not measured directly, there is also evidence that the larger troop spent more energy moving within a food patch, but not when travelling between patches.

Intergroup defense of resources may also lessen the effects of feeding competition in larger groups. A key element of Wrangham's (1980) model of

female social organization is that females form groups to defend and efficiently harvest important resources. Intergroup encounters among ringtailed lemurs lends support to this thesis. Peaks in such encounters happened at times when females would be especially motivated to defend resources, i.e. to provide food for infants during weaning, and for themselves during birth and early lactation. Such peaks have also been noted for ringtailed lemurs at Berenty (Jones, 1983). Like at Beza Mahafaly, Jones has noted that increases in aggressive intergroup encounters occurred during the latter part of the wet season when infants were weaned, and that the greatest number of intergroup encounters occurred during the birth season. It should also be noted that the peak in May coincides with the mating season, a period of considerable social unrest (Jolly, 1966) which may exacerbate intergroup encounters.

Cheney (1981) found that among free-ranging vervets (*Cercopithecus aethiops*) high-ranking vervets participated more in intergroup encounters than did low-ranking females. She argues that high-ranking females might have had more to gain from resource defense because, within their groups, they had priority of access to foods. For ringtailed lemurs, preliminary results suggest that higher ranking individuals were not involved, overall, in more intergroup encounters. Since contested resources were temporally limited (i.e. pools of water, fruits) but usually not monopolizable, low-ranking females would also benefit from intergroup encounters that increased access to these resources. However, many variables affecting involvement in intergroup encounters have not been accounted for, such as the level of participation. For example, all observed cases involving aggressive contact (jump-fights, grappling on the ground, biting) involved the top-ranking female. High participation by the younger, lower-ranking females may have also been alliances to support their mothers in such encounters.

Thus by aggressively defending or acquiring access to limited resources, larger groups may actually counterbalance the effects of intragroup feeding competition. The fact that both yearly and seasonal results indicate that individuals in the larger group actually did better, in terms of yearly fruit and total intake, excluding TIFR, and that they had greater nonTIFR intake during

the wet and transitional seasons lends support to this view. From the perspective of energy expended in processing foods, Green troop used more of the easily utilizable fruits. Decreasing foraging efficiency associated with increasing group size is predicted by the predation model for group size (Van Schaik, 1983). However, even during the dry season, when less food was available (based on phenological scores), the individuals of the larger troop did not exhibit reduced food intake nor did they have reduced feeding efficiency. Stacey, (1986) also reports no marked difference in foraging efficiency in large and small groups of free-ranging yellow baboons.

During the dry season the larger troop had greater leaf intake. In the reserve there was a disturbed patch along the riverbed which contained an abundance of *Ipomoea cairica*, and *Justicia glabra*. *Ipomoea* produces a concentrated supply of succulent leaves and flowers at a time when few such items were generally available. During the dry season this was a hotly contested area used by three different troops (Red, Blue and Green). This patch was located within both Red and Blue's normal home range, but not Green's. During the dry season only, Green troop would go on daily "foraging raids" into the area, and most of their intergroup encounters during the dry season occurred at this site. Although this patch was close to Black troop's home range, they were not observed using this area. Green troop was larger than Red or Blue troop, and this may have aided them in successfully using resources in an area not within their normal range.

PREDATOR PRESSURE AND SPATIAL BEHAVIOR

It was expected that if predator pressure affects grouping behavior (and hence group size) then as predator pressure increased (measured by percentage of sightings of potential predators) solitary behaviors should have decreased. This was not the case. In both troops, solitary activities were best explained by resource availability and use. Since leaves tend to be more widely distributed than fruits, it is perhaps not surprising that for both troops increasing leaf availability was associated with an increase in solitary foraging and feeding behavior. Indeed, given the wider distribution of leaves, the

tendency for lactating females to spend more time feeding solitarily is most likely tied to their greater emphasis on leaf feeding (see Chapter 3).

While fruits ingested were positively correlated with solitary behaviors in Green troop, this was not the case for the smaller Black troop, and may relate to the greater incidence of widely spaced fruit trees such as SAFR within Green troop's home range.

It was also expected that greater predator pressure should be positively correlated with a higher percentage of close interindividual distances. In the larger Green troop this did not occur. However in the smaller Black troop, which would presumably face greater predation pressure with fewer individuals for predator detection (Terborgh and Janson, 1986) the correlation between close nearest neighbors and predator pressure almost reached significance. This indicates that while predation pressure may have an effect on interindividual distances within smaller groups, this is substantially mitigated by resource distribution and availability.

In both troops fruit feeding had a meaningful negative correlation with close interindividual distance, suggesting that because fruit feeding is associated with greater agonism there is a tendency for individuals to perhaps try and minimize this by feeding as far apart as the distribution of the resource allows. The marked correlation between flower feeding and close interindividual distances is expected, due to the restricted distribution of major flower species (GAFL and QUFL) .

Van Schaik (1989) reasons that where intragroup competition is important, one should expect high ranking individuals to be more involved in intergroup competition, as seen in vervets of Amboseli (Cheney, 1987). Preliminary data on ringtailed lemur intergroup behavior indicate that the patterning of involvement does not support the contention that higher-ranking individuals are more involved, at least among females, because in both troops low ranking (younger) females showed high levels of involvement. This tendency does make intuitive sense, since lowest-ranking younger females have the most to lose from lack of access to resources.

Because few ringtailed lemur foods at Beza Mahafaly are distributed in such a way as to be totally monopolizable by a single high-ranking individual, high levels of low ranking female involvement may be advantageous both in terms of contest and scramble competition. Males were less involved in intergroup disputes, and male interactions were qualitatively different from female encounters. When males did participate, it involved ritualized stink-fights and chases with other males, but many males seemed to simply take advantage of female intergroup involvement by feeding in contested resources while the females were busy fighting.

As in interindividual feeding competition, the abundance and distribution of resources has a strong effect on the patterns of intergroup resource competition. Waser (1976) found very low rates of intergroup encounters among free-ranging mangabeys, *Cercocebus albigena*, and tied this to the low predictability of important, but rare and concentrated fruit resources (e.g. figs). Harrison, (1983a) did an indepth study of intergroup behavior in the vervet monkey, *Cercopithecus aethiops* within a forest and woodland environment. He produced good evidence that the distribution and availability of resources as well as their value to the group determined the intensity and duration of intergroup encounters. Specifically, the most intense encounters occurred when foods were both scarce and seasonally important. Even in Janson's (1985a, 1985b) study of brown capuchin monkeys, which found only low levels of intergroup resource defense, the effect of food distribution may have mediated such encounters. Intergroup contest competition should only occur over large, centralized resources which are defensible. It seems that there were few large fruit patches within these monkey's home ranges. In fact, he notes that when groups did fight, it was over the only large, monopolizable fruit source, i.e. fig trees.

Harrison's (1983) results indicate that in forest living species it is not just overall reduction in food availability, but rather the fluctuating availability of specific important species of fruits and flowers that may effect intergroup encounters. At Beza Mahafaly over half of the encounters resulted in the winning troop using the resource, indicating that access to food or water was

key to such encounters. Temporal availability of resources in association with critical reproductive events appears to influence the patterning of intergroup encounters. The marked correlation between decreasing food availability and increasing intergroup encounters during the wet season, indicates that troops were responding to this reduction by contesting with one another over remaining fruit patches. During the dry season, when food availability decreased and large fruit sources were not available, intergroup encounters also decreased and were maintained at a lower level until late September and October, when intergroup encounters again increased dramatically. This period also coincided with the appearance of important fruit species, *Talinella dolphinensis*, *Antidesma petiolare*, *Maurua filliformis*, and the continuing availability of *Salvadora augustifolia*, and the flowers of *Quisvianthe papinae*, and *T. indica* which first appeared during the latter part of September (see Fig. 2.4). This clearly indicates that increases in intergroup encounters are intimately related to an increase or decrease in the availability of resources, and that flowers and fruits are the most contested items. Similar trends are reported by Dittus (1987) for toque macaques, where 95% of group supplants were over access to fruit trees. de Ruiter (1986) also noted that when comparing different-sized groups of wedge-capped capuchins, the larger group had an advantage in intergroup competition as it had more exclusive use of some areas which contained fruit trees. This resulted in greater percentage use of some fruits, (e.g. *Vitex orinocensis*), by the larger group, although other troops did have access to alternative foods. For ringtailed lemurs such foods are limited both in time and quantity, and provide important food resources for lactating females and for infants undergoing weaning. Access to these resources should be and were always contested, as their abundance could be diminished by others (sensu Isbell, 1991).

Distribution of resources also mediates the level of feeding agonism within larger versus smaller troops. Individuals in larger troops do not necessarily incur greater feeding costs *if* the resource is distributed in such a way as to allow a more egalitarian access. However, when the resource is rare *and* clumped, individuals in larger groups can incur greater feeding costs. Most primate groups probably utilize a mosaic of food types and the

importance of feeding competition will be expected to alter based on the characteristics of the food patch. Any broad-based theories on the evolution of group size in primates will therefore have to reconcile with the actual complexities and variability of primate resources and their effects on resource competition.

Although predation pressure may modify grouping behavior in smaller populations, the distribution and availability of resources seems to be the most important factor in determining how individuals pattern themselves within the environment. There was little support for van Schaik's (1989) contention that predation pressure drives female social relationships, but Wrangham's (1980) model was supported. Female ringtailed lemurs incur high reproductive costs set against a backdrop of great variability in resource abundance. By grouping together, individuals within larger groups apparently are able to sustain larger numbers by defending resources from other groups, and in some cases larger groups fare better during stressful periods such as weaning and birth season. Resource defense thus seems to be an important characteristic of female resource competition in environments of variable resource availability.

CHAPTER 6

INDIVIDUAL VARIABILITY IN RESOURCE USE

INTRODUCTION

Determining the life-history strategies of individuals provides an important building block upon which to develop a better understanding of larger issues such as foraging behavior and reproductive success. Unfortunately much of such behavior is anecdotal and does not lend itself easily to quantitative analyses. Nevertheless, the study of individual behavioral variability potentially can give us a more indepth understanding of how individuals with different abilities, strengths and weaknesses coexist within a group. In this chapter interindividual behavioral variability in foraging styles and general behavior is presented.

RESULTS

INDIVIDUAL TACTICS

Behavior of Low-ranking Individuals

The previous chapters have attempted to illustrate how various ecological and social factors affected the behavior of classes of individuals in Green and Black troop. There were also individual behaviors which may be personal responses to such factors. One of the most striking behaviors was the tendency for lower-ranking individuals to attempt to acquire access to rare and highly-contested resources by either arriving first, or by foraging on these resources by themselves. Ringtailed lemurs appear very familiar with fruit trees within their home ranges and travel was primarily to move from one patch of fruit or flower trees to another. Once the troop had begun its progression, individuals seemed generally to know where they were headed. When the resource was a fruit tree, e.g. *Grewia* sp. lower-ranking females or males would race ahead of the rest of the troop, and were already in the trees

feeding when the remainder of the troop arrived. In Green troop, two members, male 50 and female 53, commonly used this tactic. However once the rest of the troop arrived, these individuals could be and were displaced by higher-ranking members.

Lower-ranking individuals might also feed by themselves, as long as they knew the location of the rest of the troop. For example, on October 12, 1988 female 53 left the rest of the troop feeding on fruit in a *Tamarindus indica* tree, and travelled by herself for 1/4 ha to a richer feeding area. There she was able to feed on the fruit of *Catanaregam spinosa* (a rare and dispersed fruit tree) as well as a large patch of new red leaf buds of *T. indica*. She fed quickly while alone, and then raced back to the rest of the troop.

Other individual tactics involved the use of specific foods or food parts. Tables 6.1 and 6.2 show the mean weights in grams for food parts consumed by each individual. Low-ranking males focused on TIFR as an important resource (Wet Season, Black Troop: 19; Green Troop: 86, 70; Dry Season, Black Troop: 19) and the lowest ranking females of both troops (Black troop: 62; Green troop: 93) had high intakes of TIFR during the dry season when food availability was drastically reduced. TIFR was not associated with high levels of feeding agonism and was not patch-dependent. Because they were large fruits which could be removed from a feeding patch, individuals probably did not incur as high a feeding cost when displaced from TIFR patches. Low ranking females also fed more on food parts associated with less feeding agonism, such as leaves, during the dry season (Black troop: 42, 62; Green troop: 53, 73, 93).

Table 6.1. Total weights of top 20 foods eaten by Individuals of Black troop by season.

WET SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
02	1	1.52	33.39	34.91	.62	0	2.14	35.53
82	2	.65	25.00	25.65	1.76	0	2.85	27.85
42	3	.65	10.77	11.42	1.32	0	2.14	12.91
62	4	.67	30.21	30.88	.93	0	3.55	33.76
99	5	.94	14.31	15.25	1.68	0	3.61	17.92
19	6	.93	57.24	58.17	1.30	0	2.52	59.76

DRY SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
02	1	.20	4.77	4.97	.17	1.44	1.81	6.58
82	2	.44	14.31	14.75	.08	1.08	1.60	15.91
42	3	.24	7.95	8.19	.26	.16	.66	8.61
62	4	.24	10.63	10.87	.31	.45	1.00	11.63
99	5	.08	4.77	4.85	.48	.28	.84	5.61
19	6	.04	14.79	17.53	.10	.24	.38	17.87

Table 6.2. Total weights of top 20 foods eaten by Individuals of Green troop by season.

WET SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
13	1	1.59	6.36	7.95	1.17	0	2.76	9.12
33	2	1.83	14.31	16.14	.92	0	2.75	17.06
53	3	1.08	7.95	9.03	2.51	0	3.59	11.54
73	4	2.20	15.90	18.10	1.01	0	3.21	19.11
93	5	1.71	17.49	19.20	1.09	0	2.80	20.29
10	6	1.65	4.77	6.42	1.01	0	2.66	7.43
30	7	.96	17.49	18.45	1.26	0	2.22	19.71
50	8	1.91	6.36	8.27	1.38	0	3.29	9.65
86	9	1.66	33.86	35.52	1.81	0	3.47	37.33
70	10	1.72	17.49	32.52	.85	0	2.57	33.37

DRY SEASON

INDIVIDUAL	RANK	FRUITS WITHOUT TIFR	TIFR	TOTAL FRUIT	LEAVES	FLOWERS	TOTAL WITHOUT TIFR	TOTAL
13	1	.69	9.54	10.23	.48	.26	1.43	10.97
33	2	.38	6.36	6.74	.37	.30	1.05	7.41
53	3	.88	11.13	12.01	1.22	.32	2.42	13.55
73	4	0	6.54	6.54	.63	.53	1.16	7.70
93	5	.21	20.67	20.88	.65	.60	1.46	22.13
10	6	0	14.31	14.31	.97	.42	1.39	15.70
30	7	0	11.13	11.13	.53	.67	1.20	12.33
50	8	.06	6.36	6.72	.99	.54	1.59	7.95
86	9	0	6.36	6.36	.58	.60	1.18	7.54
70	10	.77	9.54	10.31	.82	.54	2.13	11.67

Low-ranking Lactating Females

As was noted in Chapter 4, lower-ranking lactating females may suffer the greatest feeding costs because they are not only constrained by feeding competition, but also by increasing nutritional requirements associated with lactation. Recall that lower-ranking females had more feeding losses, especially aggressive displacements, and low-ranking lactating females used more expensive forms of foraging than did higher-ranking lactating females. How might such females lessen these costs? One important tactic is to avoid feeding near the top-ranking female, who tended to be responsible for more of the feeding agonism than any single individual received (see Table 4.12 and 4.13). Looking again at nearest-neighbors (Table 6.3 and 6.4) it can be seen that this indeed is the case. Lower-ranking lactating females (female 53 of Green troop and female 42 of Black troop) spent less time feeding near the top-ranking female of their respective troops (female 13 of Green troop and female 02 of Black troop). In addition, during the critical birth and early lactation period (transitional season) these same females again spent the least amount of time feeding near the top-ranking female (Table 6.5 and 6.6). This pattern is not seen during the dry season, when all females were pregnant.

Table 6.3. Mean percentage nearest neighbors while both feed during the wet and dry season in Green troop.

INDIVIDUALS	WET SEASON	DRY SEASON
02 & 42	3	2.2
02 & 62	9.4	5
02 & 82	19.4	1.2
02 & 99	6.8	2.8
02 & 19	8.4	3.8
82 & 42	1.4	8
82 & 62	9.8	11.2
82 & 99	4	8.4
82 & 19	7.2	4
42 & 62	10	13.2
42 & 99	5.6	8.8
42 & 19	2.8	5
62 & 99	7.8	10.6
62 & 19	4	9.2
99 & 62	1	0
99 & 19	5.6	3.8

Table 6.4 Mean percentage nearest neighbors while both feed during the wet and dry season in Green troop.

INDIVIDUALS	WET SEASON	DRY SEASON	INDIVIDUALS	WET SEASON	DRY SEASON
13 & 33	3	1.8	53 & 86	3	3
13 & 53	.83	2.2	73 & 93	3.8	4
13 & 73	4.8	5	73 & 10	.33	3
13 & 93	8.2	2.2	73 & 30	0	4
13 & 10	.60	2.2	73 & 50	2	2
13 & 30	1.6	.33	73 & 70	0	-
13 & 50	.60	0	73 & 86	4	6
13 & 70*	.60	-	93 & 10	.33	3
13 & 86	4.8	1.8	93 & 30	.60	3
33 & 53	3	2	93 & 70	0	-
33 & 73	2.6	2.4	93 & 50	1	2
33 & 93	1	3	93 & 86	1.60	3
33 & 10	3.6	3.6	10 & 30	1.2	2.8
33 & 30	1	.33	10 & 70	1	-
33 & 50	1.4	1.4	10 & 50	6	3.6
33 & 70	1	-	10 & 86	2	2
33 & 86	7.8	2.2	30 & 70	.40	-
53 & 73	4	2.4	30 & 50	0	1.2
53 & 93	1.6	4.2	30 & 86	2.4	1
53 & 10	2	0	50 & 70	.83	-
53 & 30	2	1.8	50 & 86	.33	1.4
53 & 50	3	3.4	86 & 50	0	0
53 & 70	1.6	-	86 & 70	1	-

*This individual transferred to Blue Troop during the dry season.

Table 6.5. Pairwise nearest neighbors during the transitional season in Black troop.

INDIVIDUALS	TRANSITIONAL SEASON
02 & 42	2.66
02 & 62	6.66
02 & 82	15.67
02 & 99	3.33
02 & 19	6.33
82 & 42	19.67
82 & 62	7.00
82 & 99	8.00
82 & 19	3.66
42 & 62	8.66
42 & 99	5.00
42 & 19	1.00
62 & 99	0
62 & 19	6.00
99 & 19	4.66

Table 6.6 Mean percentage nearest neighbors while both feed during the transitional season in Green troop.

INDIVIDUALS	TRANSITIONAL SEASON	INDIVIDUALS	TRANSITIONAL SEASON
13 & 33	0	73 & 50	1.66
13 & 53	.66	73 & 70	-
13 & 73	3.33	73 & 86	1.66
13 & 93	12.33	93 & 10	2.66
13 & 10	.66	93 & 30	3.66
13 & 30	3.00	93 & 70	-
13 & 50	0	93 & 50	1.66
13 & 70*	-	93 & 86	3.33
13 & 86	2.33	10 & 30	0
33 & 53	0	10 & 70	-
33 & 73	5.66	10 & 50	2.66
33 & 93	4.00	10 & 86	2.66
33 & 10	5.00	30 & 70	-
33 & 30	.66	30 & 50	.66
33 & 50	.66	30 & 86	2.66
33 & 70	-	50 & 70	-
33 & 86	2.33	50 & 86	4.00
53 & 73	1.00	86 & 50	4.00
53 & 93	2.66	86 & 70	-
53 & 10	0		
53 & 30	1.00		
53 & 50	.66		
53 & 70	-		
53 & 86	3.33		
73 & 93	6.67		
73 & 10	2.66		
73 & 30	.66		

*This individual transferred to Blue Troop during the dry season.

Individual Reaction to Attempted Male Transfer

From February to May, 1988, a new male, 60, attempted to transfer into Green troop. Although this male was not successful and eventually transferred into neighboring Blue troop, during this period he spent most of his time with Green troop. There was interindividual variability in agonistic behavior directed toward male 60 by members of Green troop. Table 6.7 breaks down the agonism received by male 60 by individual and context. Surprisingly, the individual showing the most agonism toward this new male was not the top-ranking troop male, 10, but rather female 53. She had the greatest proportion of agonistic events directed toward male 60, with most of these encounters over food.

Table 6.7. Proportion of Agonism Between Transferring Male, 60, and Members of Green Troop.

Dyad	Agonism	Context		
		Feed	Space	Stink-flight
53 & 60*	37	34	2	0
93 & 60	16	11	5	0
10 & 60	11	8	0	3
33 & 60	11	3	8	0
13 & 60	11	8	3	0
50 & 60	8	3	5	0
86 & 60	0	0	0	0
70 & 60	0	0	0	0
73 & 60	0	0	0	0

*Significantly greater at $p < .05$ than all other dyads.

BUFFER EFFECTS

Results reported in Chapter 4 did not indicate a clear relationship between high social rank and greater food intake. Only those resources which were monopolizable showed clear rank effects. An important advantage of high rank which has not received much attention in the literature, is the effect the rank of a mother has on the feeding success of her offspring. In this study four adult mother-daughter pairs (Green troop: high-ranking mother, 13-93; low ranking mother, 53-73; Black troop: high-ranking mother, 02-82; low ranking mother, 42-62) and one adult mother-son pair (high-ranking mother, 33-86) were known. These offspring were two years old at the start of the study and all the daughters successfully mated and produced their first offspring during the study period.

In the ringtailed lemurs studied here, adult offspring (82, 62, 73, 93 86) tended to feed markedly closer to their mothers than other individuals when food was more abundant (wet season, transitional season) (see Tables 6.5, 6.6), yet they received less feeding agonism from their mothers (see Tables 4.12 and 4.13, Chapter 4). High ranking females may have provided a foraging "buffer zone" wherein she and her offspring exclusively fed, but which was avoided by others. Two examples may illustrate this. On one occasion female 73 attempted to steal a fruit of *T. indica* (TIFR) from male 86, but 73 was threatened away by his mother, female 33. On another occasion the troop was feeding on an isolated patch of herbs (MCLV). All of the females fed, but they actively kept most males out of the small patch. The only exception was male 86, who was able to feed near his mother, 33. The rest of the males had to wait until the females had finished. If animals have to wait, then by the time they have access to a food patch the rest of the troop may move on and such individuals would not get to feed.

During the dry season, although offspring did not spend as much time feeding near their mothers, they continued to be buffered in that they were involved in decidedly less aggressive feeding agonism from their mothers (daughters and son; see Tables 4.12, 4.13, Chapter 4). Comparing daughters of high-ranking versus lower-ranking females (Green troop: 93 versus 73; Black

troop: 82 versus 62) also indicates that the former were involved in less aggressive feeding during both seasons (see Fig 6.1).

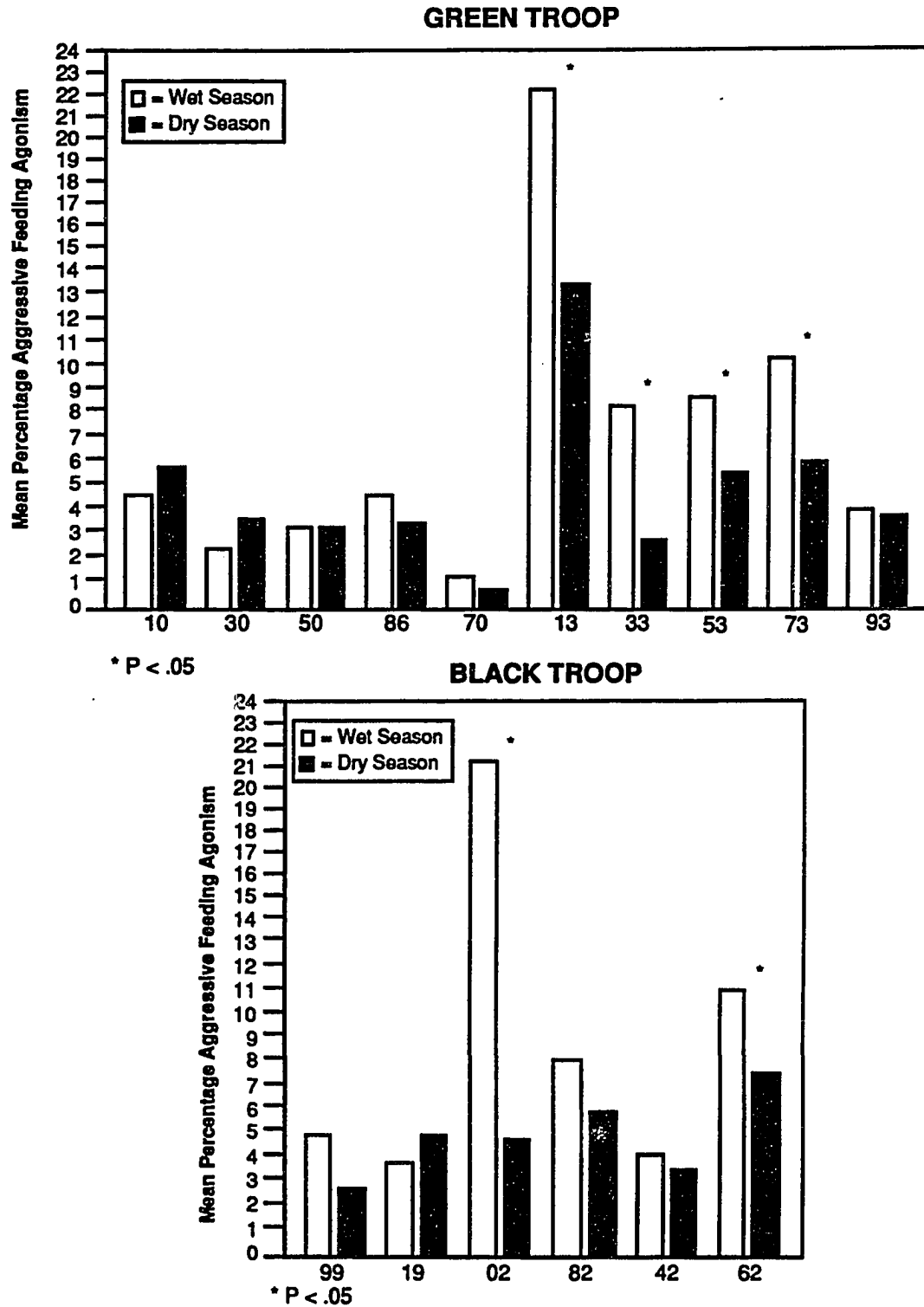


Figure 6.1. Mean Percentages of Time Involved In Aggressive Feeding Agonism During the Wet and Dry Seasons.

These patterns suggest that having a high ranking mother may depress the percentage of aggressive feeding disruptions received even by adult offspring, and that this could result in such individuals having greater food intake since time spent in feeding agonism means less time feeding and more energy expended. There is evidence of this.

Food Intake

As argued above, if offspring are buffered from high levels of feeding displacement they may be able to feed more and thus increase food intake. Tables 6.1 and 6.2 reproduce tables from Chapter 4 to show total minimum weights for the top 20 foods eaten in the study troops. During the dry season daughters (Green troop: 93, 73; Black troop: 62, 82) had higher total minimum intake than did their mothers. Furthermore, daughters of highest ranking females (Green troop, 93; Black troop, 82) had the greatest total intake relative to females and most males. The mother-son pair (33 and 86) did not show this pattern.

During the dry season total fruit intake by weight was greatest for the daughters of the top-ranking females (Green: 93; Black: 82). This was due to higher TIFR feeding by 93 and by both high TIFR and non-TIFR fruit-feeding by 82. Female 93 also ingested a higher mean weight of flowers.

Use of specific resources also varied depending on the rank of the mother. Although intake of *Grewia* sp was greater for higher-ranking females, there was one exception. Female 93, the daughter of 13, had higher minimum weights than might be expected based on her rank (see Table 4.23, Chapter 4). Similarly, 02's daughter, 82, had a higher intake of QUFL flowers than even her mother (.09 grams versus .01-.05 grams; see Table 4.22).

Feeding Efficiency

Another indication that offspring might be buffered from feeding competition is with respect to feeding efficiency. If offspring feeding near

their mothers suffered fewer feeding displacements, then this should have resulted in higher efficiency ratios, i.e. they should have spent more time feeding and less time looking for new food patches. Overall efficiency ratios are presented in Table 6.8. A clear advantage for higher-ranking female's offspring can be seen. In Black troop, female 82 (daughter of 02) had the highest female efficiency ratio in the wet season. In Green troop, male 86 (son of 33) had the highest efficiency ratio in the wet season and female 93 (daughter of 13) had the top feeding efficiency ratio in the dry season. Offspring of lower-ranking females (73, daughter of 53; 62, daughter of 42) did not show this advantage. Comparing female 93 of Green troop and female 62 of Black troop, maternal differences become clear. Both of these females were the lowest-ranking in their respective troops, but female 93 was the daughter of the top-ranking female, while 62's mother ranked much lower. Female 62 suffered much higher agonistic feeding losses than did female 93 (see Fig. 4.11).

Table 6.8. Feeding efficiency ratio for Green and Black troop.**BLACK TROOP**

Individual	Rank	Wet	Dry
02	1	.75	.42
82	2	2.90	.67
42	3	1.15	.81
62	4	1.65	.69
99	5	.35	.35
19	6	6.00	.58

GREEN TROOP

Individual	Rank	Wet	Dry
13	1	.89	.53
33	2	1.38	.32
53	3	1.33	.44
73	4	1.20	.34
93	5	1.40	2.09
10	6	1.57	1.08
30	7	1.25	.44
50	8	.91	.22
86	9	3.52	1.00
70	10	3.12	1.30

*Ratio of 1 = equal time spent feeding and foraging. The higher the ratio, the more time spent feeding relative to foraging.

DISCUSSION

STRATEGIES OF LOW-RANKING INDIVIDUALS

Male dispersal is common among primates, and may be tied to intrasexual competition, and increasing mate access (Pusey and Packer, 1987). These appear to be less important factors for females, and female dispersal is rare. Nevertheless, it might be expected that if feeding competition is too great for low-ranking females, then they should transfer to troops with reduced resource competition, e.g. those with fewer males, troops living in richer areas etc. However costs associated with transfer are presumably great, and may include greater predation pressure, loss of affiliative ties, and in dimorphic species smaller females may be at a competitive disadvantage (Dittus, 1986; Pusey and Packer, 1987). Groups could also fission, with low-ranking matriline forming a new group (Chepko-Sade and Sade, 1979, Koyama, 1970). However, such new groups might still be at a disadvantage if they were unable to defend resource access or were forced into lower quality habitats (Isbell, et al., 1990). Alternatively, low-ranking individuals may remain within a troop and mediate these disadvantages of rank by employing certain tactics.

Van Noordwijk and van Schaik (1987) noted that among long-tailed macaques, "low-ranking females can compensate for a feeding disadvantage in the main party by leaving temporarily" (p. 587). Low ranking individuals feeding outside the main party had similar fruit picking rates as higher-ranking individuals in the main group.

Deutsch and Lee (1991) also noted different feeding tactics among lower-ranking rhesus monkeys in captivity. Lower-ranking females ate more of their food away from the main food site and fed more rapidly. They also took advantage of their cheek pouches, by stuffing them with food pellets and then eating away from the main feeding area. Thus although subordinates

received more agonism when in the feeding area, their overall intake was not markedly different from dominant females.

Post et. al (1980) have pointed out that "low ranking individuals may preferentially include certain foods in their diet or use certain feeding sites precisely because of the low probability of supplantation from these foods or sites." (p. 189). Janson (1985a) noted just such an effect among brown capuchin monkeys. He found that some subordinate individuals were able to markedly increase their energy intake by eating more dispersed foods (i.e. insects, seeds, or frond pith).

Low-ranking ringtailed lemurs in the study troops employed a number of these tactics. Their feeding repertoire included feeding in richer patches away from the main group, as well as entering feeding trees before others. The latter was an especially viable tactic for food resources that were rare and monopolizable. If lower ranking individuals simply waited for others to finish, there might be few ripe fruits left, and by the time they were able to enter such resources the rest of the troop might move on. Individual members were extremely reluctant to remain behind if the troop had begun travel to another site, and therefore these individuals might not be able to feed in these patches at all.

Lower-ranking individuals also focused on food resources that were associated with less feeding agonism, such as TIFR and leaves during the dry season. Lower ranking lactating females may have also attempted to minimize feeding costs during the wet season by avoiding feeding near the highest-ranking female, where displacements from food were more likely. This was a viable strategy given that both female 53 and female 42 were lactating at this time, that lactation is a costly endeavor, and that these females did not have priority of access to all food sites as did the higher ranking females.

The reaction of individuals to an attempted transfer by non-troop males has been observed by Sussman (1972, pers. comm.) who noted it was

primarily females who chased new males to the periphery of the troop. This was also seen in this study. The lower-ranking lactating female, 53, of Green troop was responsible for a disproportionate amount of agonism directed toward a male attempting to transfer, and more of these encounters were over food. Since this new male would be an additional source of feeding competition, specifically to low-ranking females who encountered more direct feeding competition from males during the dry season (see Chapter 4), females, especially low-ranking ones, may attempt to limit male transfer. Indeed, this male did not successfully transfer into Green troop. In sexually dimorphic species females sometimes form coalitions to drive off males attempting to enter a group (Smuts, 1987) or to acquire a feeding patch from a male (Cheney, 1983).

BUFFER EFFECTS

The relationship between rank and reproductive success in female primates has been investigated in a variety of primate species with varying results (Silk, 1987b). Of the various measures of reproductive success, survival of offspring has been positively associated with higher dominance rank in a number of species (Silk, 1987b). The *mechanism* by which this occurs has yet to be clearly investigated, but may be tied to resource access. If high-ranking members tend to favor some, but not all individuals feeding near them, this could then affect individual feeding success. Studies which have focused on spatial relationships during foraging suggest that kin-relatedness may be a factor.

A number of researchers have explored the importance of kin-relatedness during feeding in Japanese monkeys (*Macaca fuscata fuscata*) at Koshima, Japan with varying results. Early work by Kawai (1965) first reported higher instances of co-feeding (animals feeding side-by-side in a food patch) between kin, and this included adult offspring as well. Demographic patterns of Japanese macaques at Koshima studied by Mori (1979) showed that high ranking female's offspring (aged 6-7 years old) who were born during a non-provisioned period were heavier in body weight than offspring of lower-

ranking females. In addition, most surviving juveniles born during the non-provisioned period were offspring of high-ranking females, indicating to Mori that "Offspring of mothers of high status enjoy advantages in feeding on available food resources (fruit and artificial food)" p. 388. Iwamoto (1987) found that individuals up to the fourth degree of kin-relatedness were allowed to feed near a focal animal, but that once an interaction occurred, kin-relatedness had no effect on the severity of the interaction. However, Ihobe (1989) in a 1 month study of 9 individuals during a period of food abundance did not find kinship (up to the third degree of relatedness) to be important in effecting whether the individual entered a feeding patch, nor whether the focal animal remained in the patch and fed.

In a study of Japanese macaques on Yakushima Island (*M. fuscata yakui*) Furuichi (1983) found that both frequency and severity of agonism varied by kinship. Kin-related females had few agonistic interactions, and kin-related individuals were able to approach one-another without agonism. Furthermore there were no differences among kin related to rank as to who did the approaching, i.e. subordinates were just as likely to approach dominant kin as vice-versa, whereas dominant females tended to approach unrelated subordinate females more often. He concluded that because Japanese macaques fed further away than the distance wherein feeding agonism usually occurred, co-feeding advantages between kin would probably only be important when food resources were reduced. However, he took no account of the seasonal changes in food distribution nor patch use, as the study period was only one month. Finally, artificial feeding for Japanese macaques at Mt. Ryozen, was found to exacerbate an already existing pattern of greater survival of infants of high-ranking mothers (Sugiyama and Ohsawa, 1982). When provisioned, higher-ranking females had even greater infant survival rates.

Evidence of "feeding nepotism" (Iwamoto, 1987) has also been noted in other primate species. Dittus (1986, 1987) reported that when one troop of toque macaques took over another troop's range and fused with them, the result was that all of the female members of the subjugated group, with the

exception of one offspring, died. This was most likely due to the fact that the invading troop maintained its priority of access to resources even after fusion.

Robinson (1981) also noted that when wedge-capped capuchin monkeys fed in a monopolizable resource such as a fruit tree the top-ranking male and female excluded most animals except offspring of the alpha female and some juveniles.

Among vervets, Fairbanks and McGuire (1986) have shown that continued social support of adult female offspring by their mothers is both socially advantageous (helping their adult daughters acquire rank), and affects a daughter's reproductive success. Young adult females without mothers had a lower fecundity rate and a much higher infant mortality rate. Among semi-free-ranging *Lemur catta* a positive relationship between a mother's rank and the reproductive success of her daughter has been found (Taylor, 1986). Exactly how this occurs appears to be complex, but may include reducing the amount of aggression and harassment a daughter receives (Silk, 1983, Fairbanks and McGuire, 1986). Since reproduction is most likely tied to the availability and quality of food resources, mothers may also improve the feeding behavior of their adult offspring. In this study adult offspring of high ranking females showed feeding advantages even greater than their high-ranking mothers. Many of these occurred during a stressful period (i.e. the dry season when females were pregnant and when food was less available). Such advantages were not seen among adult offspring of lower ranking females. The results of this chapter and chapter 4 indicate that although behaviors associated with high rank may be costly, because such individuals may expend more energy in feeding agonism, this behavior may also buffer adult offspring from high levels of feeding competition.

CHAPTER 7

CONCLUSIONS

Our basic understanding of the Malagasy lemurs has been built upon numerous important studies (Jolly, 1966; Sussman, 1974; Pollock, 1977; Richard, 1978; Charles-Dominique, et al, 1980) including those which have documented the general behavior and ecology of ringtailed lemurs (Jolly, 1966; Sussman, 1974, Budnitz and Dainis, 1975; Jones, 1983). However, long-term field studies have provided strong evidence that individuals vary their behavior throughout their lives. For example, males may alter their tactics to acquire mates depending on their age (Smuts, 1985), and dominance relationships can change over the course of a lifetime (de Waal, 1987). Understanding how proximate factors such as reproductive state or rank affect reproductive or feeding success is critical to the development of cogent evolutionary theories (Cheney, et al, 1987). This emphasis on life-history patterns makes it essential that studies now document the role of individual factors as well. This has been my goal.

REPRODUCTIVE SEASONALITY AND RESOURCE AVAILABILITY

While all females must face the demands of reproduction, in a seasonal environment these pressures may be especially acute (Pollock, 1977). For example, Chism, et al. (1984) report that among a free-ranging population of patas monkeys, 34% of the reproductive females died during a lengthy period of extreme drought. This was much higher than other age-sex classes. Each of these females was lactating or pregnant, highlighting the vulnerability of reproducing females to ecological events. How these reproductive constraints affect female behavioral ecology may provide insight into other aspects of female behavior. Ringtailed lemurs live within a strictly seasonal environment, with a period of food abundance (in normal, nondrought years) and a period of reduced food availability. Much of their behavioral ecology appears tied to this basic pattern. Females within a troop all lactate and wean their infants during the period of food abundance, insuring in normal years that they can successfully meet the demands of this most costly

reproductive state, and that there will be ample weaning foods available (Altmann, 1980). They are thus pregnant when food sources are reduced, which has been shown to be a less costly reproductive state for other species (Clutton-Brock, et al, 1989). In this sense ringtailed lemur reproductive seasonality is intimately tied to their environment.

This close tie between reproduction and food availability also means a potentially high level of feeding competition between females (scramble, if not contest), since most will lactate at the same time. Both intra- and intergroup behaviors help mediate this. Lactating females avoid feeding near one another, spend more time feeding away from others, and focus more on foods associated with less foraging costs and agonism (e.g. young leaves). Females of a group band together against other female groups to help insure access to important but limited resources within their environments at critical points in their reproductive cycles.

A relationship between reproduction and food availability has also been noted for other seasonally breeding primate species. Comparisons with *Cercopithecus sp.* inhabiting similarly seasonal environments is especially instructive. Butyniski, (1988) recently addressed the relationship between birth seasonality and resource availability in guenons. Savanna and woodland species experiencing one wet season with limited rainfall (35-101 cm.) compares quite well with results for *L. catta* which also had a single wet season during which 52.2 cm of rain fell. Groups living in locations with a single wet season had even shorter birth seasons than those with bimodal rainfall (2.6 months versus 5 months). In *Cercopithecus aethiops*, for example, the birth season lasts 1-3 months, and occurs prior to the season of food abundance, insuring that females lactate during a period of high food availability. That birth seasonality is tied to resources is supported by the absence of seasonality in provisioned vervets at a tourist lodge (Lee et al., 1986), and reduced seasonality in captive vervets (Eley, 1992).

In *Erythrocebus patas*, although rainfall is bimodal at two sites, the amount of rain is most like that found at Beza Mahafaly, with only 61-94 cm of rain falling per year. Patas monkeys give birth during the driest part of the

year, which allows infants to begin the transition from milk to solid foods during the wet season when food is more available (see also Chism, et al., 1984). Reproduction in this large-bodied species is rapid, with females giving birth every 11.8 months (Chism, et al, 1984).

Reproductive seasonality has also been noted for free-ranging squirrel monkeys (*Saimiri oerstedii*), which exhibited a breeding season that lasted 6 weeks, with high birth synchrony (65% of all births in one troop occurred during an 8-day period) (Boinski, 1987). Seasonal availability of resources (especially arthropods) occurred, with birth patterns such that infants could be weaned during a period of food abundance.

In ringtailed lemurs at Beza Mahafaly, females give birth at the end of the dry season (October-November), and there is demographic evidence indicating that ringtailed lemurs have a 1-year interbirth interval (Sussman, 1991). Given the faster maturation rate among lemurs, this insures that during nondrought years females lactate and wean their infants during a period of food abundance. Thus the particularly close interrelationship between reproductive seasonality and food abundance for ringtailed lemurs is not an unusual adaptation found only among Lemuriformes, but is merely part of a continuum of female primate responses to environmental constraints.

FEMALE DOMINANCE

There is increasing evidence that ringtailed lemurs may be adapted to live in drier, seasonal environments (Sussman, 1972; Ganszhorn, 1985). Results from this study suggest that female dominance in this species is an important part of this adaptive complex. Stresses imposed on female lemurs by having their reproductive events adapted to seasonal resource availability may be exacerbated by high maternal investment (Jolly, 1984, Young, et.al. 1990), and by social group living. Although Hrdy, (1981) has suggested that in female dominant species males may defer to females in feeding contexts to save up energy for mate competition, in ringtailed lemurs males are potential food competitors year round. Furthermore, male feeding competition may be

especially acute for lower-ranking pregnant females who must contend with close male feeding proximity during the period of lowest food availability. Within such a context female dominance can be seen as a critical behavior enabling females to coexist with more than one non-natal male in a highly seasonal environment.

Two sides of the same question must then be asked. First, why do males live together in multi-female groups wherein they suffer feeding agonism from all females, instead of forming all-male groups or foraging as solitary males. Second, because new troop males provide increasing food competition, especially to lower-ranking females, why then do females tolerate more than one non-natal male?

Multi-male membership is most likely tied 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 ($r=.78$, $p < .01$). This is most likely a reproductive strategy, because greater numbers of 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) since behavioral cues from females only occur when she is receptive (Evans and Goy, 1968, pers. obs.). Males occupying a central position are able to maintain a closer relationship with females to monitor their reproductive state, limit monitoring by other males, and to be the first to mate (Sauther, 1991). Furthermore, although females will mate with nontroop males, troop males are able to mate first (Sauther, 1991). If there is a first-mate advantage in this species (Periera and Weiss, 1991) mating 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.

Although females, especially lower-ranking ones, may attempt to limit the number of males entering a troop, ringtailed lemur groups normally contain more than one non-natal male (Sussman, 1991). Three suggested advantages 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 during weaning and late pregnancy-birth-early lactation 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. But among the ringtailed lemur groups observed, most males were less involved in intergroup encounters, and often fed on resources while females fought.

Ringtailed lemurs 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. During 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. In this sense, extra-troop males may provide lower-cost sentinels instead of simply increasing the number of females who more directly compete for resources because of reproductive synchronicity.

A third possibility may be tied to female reproductive success. The common view is that sexually reproducing 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 the ringtailed lemur, females who do not conceive during the first estrus period (24 hrs) will not have a second estrous cycle till 40 days later (Evans and Goy, 1968). Infant mortality in wild ringtailed lemurs is high (Sussman, 1991), and because these lemurs inhabit a

strictly seasonal environment (Jolly 1966, this study), reproduction is timed so that infants can be weaned during the period of food abundance. 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. In this study even infants conceived during the first estrus period, but born two weeks later than others were at a distinct disadvantage due to rapid infant development. In both troops these were infants born to lower-ranking multiparous females (females 53 and 42). For example, during troop progressions these infants attempted to be carried at a time when other infants were moving independently. On numerous occasions female 53 lost contact with her infant, who lagged behind, requiring her mother to come back and retrieve her. Such infants were also required to compete with other infants whose foraging skills were more advanced (Sauther, pers. obs.). Both of these infants disappeared by the beginning of the dry season. Since *L. catta* females have such a narrow reproductive "window", mating with more than one male 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 indicates that there may be a disparity in the number of males that females of differing ranks may tolerate.

It is becoming clear that the expression of female dominance in polygamous lemur species is variable. For example, Sussman (1972) found no indication of a dominance hierarchy, and low levels of aggression in *Lemur fulvus rufus*, a species similar in body size and proportions to *L. catta* (Tattersall, 1982). Pereira, et al, (1991) found no evidence of female dominance in any context for semi-captive or wild red fronted lemurs *L. f. rufus*. Recent research on sympatric populations of crowned lemurs, *Lemur coronatus*, and Sanford's lemur, *Lemur fulvus sanfordi*, also indicate variability. While both species show low levels of intragroup agonism, female dominance is clearly expressed in Sanford's lemur, but much less so in free-ranging crowned lemurs (Freed, pers. comm.).

Overt expression of female dominance may be tied to the availability of resources. The populations of Sanford's lemur and crowned lemurs studied by Freed suffered no marked seasons of fruit reduction, and were able to use a continuous supply of nonindigenous *Lantana sp.* as a food resource when other foods were unavailable. Smaller group sizes in Sanford's lemur, the tendency for the crowned lemurs to split into smaller subgroups during foraging, and greater resource availability for both species may further reduce intra-group agonism (Freed, pers. comm.).

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 *L. f. 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 moister western and eastern portions of the island (Tattersall, 1982). Sussman (1974) has suggested that red-fronted lemurs are adapted to foraging in continuous canopy where resources are more abundant and evenly distributed, whereas ringtailed lemurs are adapted to drier, more seasonal forests where foods are more sparsely distributed. Within this more seasonal environment, *L. catta* females may also suffer greater post-natal maternal costs than *L. f. rufus* females, as ringtailed lemur infants exhibit a more precocial rate of development (Sussman, 1977). Thus the red-fronted lemur may suffer less feeding pressure, leading to low levels of agonism and more egalitarian social relationships. Among ringtailed lemurs, 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.

Although not well understood or documented, there is evidence that particular ecological and biological conditions can lead to more unusual patterns of male-female social relationships among other primate species. At

least three other polygamous primate species, and one polygynous one-male species exhibit some individual female dominance over males, as well as female coalitions directed toward males. These are *Cercopithecus talapoin*, *Saimiri sciureus*, *Cercopithecus aethiops* and *Erythrocebus patas* (Baldwin and Baldwin, 1972; Wolfheim, 1977; Cheney, 1983; Smuts, 1987). Like *L. catta* both *C. talapoin* and *S. sciureus* exhibit reproductive seasonality, low percentages of sexual dimorphism, constrained mating seasons characterized by considerable male mating competition, and seasonal reduction in resource availability (Baldwin and Baldwin, 1972; Gautier-Hion, 1973). In these two species females segregate males from the main body of females except during the mating season (Baldwin and Baldwin, 1972; Rowell, 1973; Rowell and Dixson, 1975; Wolfheim, 1977). Both are small in body size and depend on cryptic behaviors, vigilance and flight as antipredator tactics (Gautier-Hion, 1973; Terborgh, 1983).

In larger-bodied vervet monkeys, reproductive seasonality is also seen (Butynski, 1988). This species is characterized by a relatively lower percentage of sexual dimorphism and seasonal resource availability (Cheney et al., 1988). Males are not segregated by females, but females can and do dominate males by forming coalitions (Cheney, 1983). Larger numbers of group males may be adaptive as there is evidence of high predation in this species (Cheney et al., 1988).

Patas monkeys inhabit highly seasonal environments, with annual rainfall similar to ringtailed lemurs at Beza Mahafaly (Butynski, 1988). Reproductive seasonality occurs, with most births occurring during a single 10-week period, and median interbirth intervals are 11.8 months (Chism, et al, 1984). Females form successful coalitions against the larger males (Loy, 1981; Chism, et al, 1984).

Whatever the cause for high reproductive seasonality (most likely resource availability, see Butynski, 1988) under these conditions females may be less able to tolerate male feeding competition. In polygamous species, reduced sexual dimorphism and female coalitions allows females to determine resource access, and will make a multi-male group structure less

expensive for the home range to support (Geist, 1974). In one-male groups living in seasonal environments, such as the patas monkey, females may reduce direct male resource competition by having only one resident male against whom they can form successful coalitions. In some populations, an influx of males is tolerated during the mating season, but males form all-male groups, or are solitary at other times of the year (Harding and Olson, 1986; Chism and Rowell, 1986)

In smaller, semi-terrestrial species such as ringtailed lemurs, male membership may still be important as an antipredator strategy, but due to a combination of high maternal investment and extreme resource and reproductive seasonality, male feeding competition is then mediated by individual female dominance. One key element appears to be whether important resources are predictable and defensible. For example, the much larger savannah baboon species (*Papio cynocephalus*), inhabits the same general areas as vervets, yet these baboons are polygamous, they are highly sexually dimorphic, in spite of seasonal changes in overall food availability there is no birth seasonality, and females rarely form coalitions against males (Cheney, 1983, Smuts, 1987, Barton, 1989). Baboon foods may be more seasonally unpredictable, and many of their food resources tend to be highly dispersed foods such as flowers, underground bulbs, corms and seeds. As such there is little advantage in defending most food resources either within or between groups since individuals can potentially move to another patch (Brown, 1964). Although Barton (1989) produces some evidence for high rank advantages when feeding on clumped resources (primarily during the dry season), because females give birth at differing times of the year, it is not clear how strong an effect this might have on an individual female's reproductive success. Nevertheless such interspecific variability within similar environments indicates that ecological and biological factors may work in complex ways to affect female-male relationships.

RESOURCE DISTRIBUTION

The distribution of resources (both spatially and temporally) has been long recognized as an important ecological variable affecting a number of social

elements, including the degree of polygyny (Clutton-Brock and Harvey, 1978), grouping behavior during foraging and feeding (Leighton and Leighton, 1982), rates of intergroup encounters (Waser 1976) and social rank advantages (Wrangham, 1981; Whitten, 1983). Although rank has often been positively correlated with access to resources, again resource distribution affects the expression of such advantages, with high rank being positively associated with access to monopolizable resources. When primates are provisioned, access to these clumped resources becomes clearly rank dependent, with higher ranked individuals having greater feeding times (Brennan and Anderson, 1988; Iwamoto, 1987; see also Fa, and Southwick, 1988). Nonprovisioned studies report similar results (Whitten, 1983; Wrangham, 1981).

Under natural conditions, rank-related feeding advantages are more difficult to evaluate. Clearly, the architecture of the feeding environment affects feeding competition. When a food patch contains many feeding sites (e.g. large-crowned trees, groves) individuals can move into alternative patches if displaced. When it contains fewer feeding sites, and all of these are monopolizable, (e.g. a water source, a single small fruit tree) higher ranked individuals can affect access to the resource, which can result in clear, rank-related differences in resources use. Even under conditions when high rank would be expected to be advantageous, such as during periods of low food availability, resource distribution mediates rank effects. Thus during the dry season, high rank was not associated with greater fruit feeding among ringtailed lemurs due to reduced fruit resources, and to its more random distribution. However, the *cost* of foraging during the dry season was most likely greater for lower ranked females who used more active forms of movement during foraging, and who had to contend with feeding competition with males who tended to be their nearest neighbors during feeding. The issue is further complicated by feeding strategies that may increase a low-ranking individual's access to rare, high energy resources such as fruits. This includes being the first to reach (and feed) in a valuable food patch, and to feed alone in rich, but limited patches. Overall rank effects may be more subtle, and may include increased foraging efficiency for offspring. It may well be that different ranks accord different advantages and

disadvantages, (e.g. Cheney, et. al., 1981) but that the expression of these within a feeding context will depend on the distribution of resources within the environment.

MODELS OF FEMALE SOCIALITY

L. catta troops are made up of kin-related females and offspring which have a high degree of reproductive synchrony and a seasonal resource base. Thus it is perhaps not surprising that this species accords well with the classical concept of a female-bonded group (Wrangham, 1980). However, unlike the model's prediction, ringtailed lemurs did not switch to a diet of low quality foods distributed in large patches when food abundance was reduced. Instead the two troops diverged in tactics. The larger troop surreptitiously invaded a rich patch of food along the river within another troop's home range, while the smaller troop concentrated on the fruit of *Tamarindus indica* and remaining patches of ground herbs. Both troops quickly made use of flower and fruit resources as they became available during the end of the dry season. Isbell's (1991) modification of the resource defense model suggests that whenever foods limit female reproductive success, and food abundance can potentially be reduced, either through contest or scramble forms of competition, females should always aggressively defend resources. Within groups, the distribution of foods should affect feeding competition. Ringtailed lemurs follow this general pattern with one caveat. During the dry season intergroup competition was reduced considerably, suggesting that when foods became scarce and perhaps less predictable (and hence less defensible) advantages of group defense were also reduced.

Female sociality in ringtailed lemurs was more closely tied to resource defense than to predation pressure (van Schaik, 1989). Predator pressure was a poor predictor of solitary feeding, which was better correlated with resource availability. Intergroup encounters were well correlated with the availability of defensible resources. Nevertheless, in the smaller troop there was a trend toward closer nearest neighbor distances and increasing predator pressure, and it may well be that female sociality is a complex response to both factors.

Other variables besides group size may also be important. For example, the large harrier hawk *Polyboroides radiatus* tended to be found in more open areas, whereas the smaller raptors were found in closed canopy trees along the rivers edge. The larger raptors may favor hunting in more open areas (Sauther, 1989) and this could affect predator pressure on different troops. There appears, however, to be no general correlation between troop size and location of home ranges (in open, drier portions of the reserve versus closed canopy riverine areas).

In conclusion, female dispersal is rare among primates, and yet for most diurnal species group life may be expected to create higher levels of resource competition. How females respond to such stresses depends on a number of ecological factors. At the forefront is the distribution and availability of resources, which determines the expression of rank advantages, reproductive seasonality, and the value of intergroup resource defense. When resources are highly seasonal, predictable occurrences which are important to specific reproductive or life-history events, reproductive seasonality may be promoted. If reproductive costs are high enough, rare forms of female-male relationships may occur. Within this context female dominance may preserve a polygamous social structure and all the advantages it confers, while limiting feeding competition received from males. Such effects should not be viewed as unique to only certain groups (i.e. the Lemuriformes), but rather as adaptations to a particular suite of ecological constraints.

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