A NEW INTERPRETATION OF THE SOCIAL ORGANIZATION AND MATING SYSTEM OF THE RINGTALED LEMUR (*LEMUR CATTA*)

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ABSTRACT

Long-term and intensive studies of identified individuals have enabled us to reexamine the social structure and organization of *Lemur catta*. Ringtailed lemurs have highly overlapping home ranges which vary in size depending upon season and habitat, and should not be considered strictly territorial. This species lives in female-resident, multimale groups centered around one dominant female who appears to be the focal point of other group members. Groups average around 13 individuals (range: 5-27) with generally equal adult sex ratios. Upon reaching adulthood, all males emigrate from their natal group and older males transfer between groups at an average of every 3-5 years, though some males have remained in the same group for at least 6 years. Males within a group can be differentiated based on natality, social status, and relationships with females. In groups intensively studied, a single, non-natal "central" male has been identified. Such males interact with females at greater rates, and are the first to mate. Females exhibit mate choice, rejecting closely related males, and actively mating with non-troop males, which results in a number of male mating strategies.

INTRODUCTION

Recent longterm studies of groups of ringtailed lemurs at Beza Mahafaly Special Reserve, Madagascar have allowed us to update and clarify certain aspects of the social structure and organization of *Lemur catta*. Beza Mahafaly reserve has been maintained as a guarded reserve since 1978. It consists of two parcels, one which contains a continuous deciduous and semideciduous riverine forest. This parcel is inhabited by 9 groups of ringtailed lemurs which have been collared and tagged so that all adults are individually identifiable. The habitat is very seasonal, with a specific hot/wet season and a cool/dry season. Social groups of ringtailed lemurs were initially characterized as multi-male, multi-female, with a central core of females, juveniles, and high-ranking males moving together, and a close-knit subgroup of subordinate adult males ("the Drones' Club") lagging behind the core of the group (Jolly, 1966). Now, studies of marked and identified groups at Beza Mahafaly have allowed us to refine this description. *Lemur catta* has also been characterized as territorial (e.g., Klopfer and Jolly, 1970; Mertl-Millhollen et al., 1979; Mertl-Millhollen, 1988). We believe this is not true, and involves a problem of

Lemur Social Systems and Their Ecological Basis, Edited by
P.M. Kappeler and J.U. Ganzhorn, Plenum Press, New York, 1993

definition. Recently, it has been theorized that the social organization of ringtailed lemurs is the result of adaptations to prevent infanticide (Pereira and Weiss, 1991). We discuss an alternative theory which we believe to be more representative of what is currently known of ringtailed lemur mating systems (Sauther, 1991).

Social Structure

Spatial Relationships of *Lemur catta* Groups. By social structure, we are referring to the size and composition of groups (group structure) and the population demography and dispersal of groups within the population (population structure) (Rowell 1972, 1976). *Lemur catta* groups average 13 to 15 individuals and range in size from 5 to 27. Adult sex ratios are close to 1.0 (Jolly, 1966, 1972; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Mertl-Milhollen et al., 1979; Jolly et al., 1982). At Beza Mahafaly, where we have followed 9 groups for 6 years, the number of both adult males and females within groups have ranged from 2 to 8 individuals. In 53 groups censused in the wild, the average number of adult males per group is 4.0 and that of females is 4.75 (Jolly, 1966; Sussman, 1974, 1991; Budnitz and Dainis, 1975). Eighty to eighty-five percent of females give birth each year, and mortality rate for the first year is between 30 and 50%, depending upon the year and locality (Mertl-Millhollen et al., 1979, Jones, 1983; Sussman, 1991, 1992).

Home ranges of ringtailed lemurs overlap, with little or no areas of exclusive use (Sussman, 1991). The size of ranges varies with habitat and location, with averages at different localities ranging from 10 to 32ha (range: 6-35ha). At different sites, population densities vary from 17.4 to 350 animals per km^2, and biomass has been estimated between 50 and 700kg per km^2.

Larger home ranges and lower densities are found in drier or more disturbed habitats (Budnitz and Dainis, 1975; O'Connor, 1987; Sussman, 1991). For example, at Beza Mahafaly groups living in drier habitats have home ranges averaging 32ha, whereas those in wetter habitats average 17ha. Group sizes in the two habitats are not significantly different. However, groups with small home ranges expand their range during certain months to feed on particular trees that come into fruit and which are absent from their normal home range (Fig. 1).

There has been some confusion as to how to define the spatial relationships of ringtailed lemurs. For example, using earlier reports from Berenty, Mitani and Rodman (1979) listed *Lemur catta* as the only primate species with multimale groups that is territorial. Because groups at Berenty have highly overlapping ranges, Jolly (1985:151) considered ringtailed lemurs to be a "dubious case" for territoriality and that "they are best considered intermediates like the Nairobi baboons (Mertl-Millhollen, et al., 1979, Jolly, 1966)". Further she stated (Jolly 1985:145): "We keep returning to the degree of overlap of range as the final criterion of territoriality". Currently, however, Jolly et al. (1993) consider ringtails to be territorial. We believe that this confusion is related to the lack of a reliable operational definition of territoriality, which often makes the meaning of this concept quite different in different contexts. In this light, we propose that territoriality should refer to "the active defense of individual or group home range boundaries by actual or ritualized agonistic encounters, thereby maintaining essentially *exclusive use* of the home range." (Waser and Wiley, 1980). Using this definition, we would not consider ringtailed lemurs to be territorial. There is considerable and in some cases almost total home range overlap among both Berenty and Beza Mahafaly groups, and, as Jolly (1972) has described, a number of troops may time-share sites for feeding, sleeping or resting. Furthermore, at Beza Mahafaly, groups will expand their home ranges into other group's ranges when certain rare resources are unavailable in their own home range. However, as Jolly et al. (1993) have pointed out there are core areas which are more intensely used by *L. catta* groups at Berenty, and at Beza Mahafaly these can change seasonally (Sauther, unpubl. data), but even these are used by other groups.

Intergroup Encounters. Intergroup encounters do occur but are most likely related to the defense of important but seasonally available resources (Sauther, 1992), and the maintenance of group integrity (Sussman, 1974). Table 1 depicts the

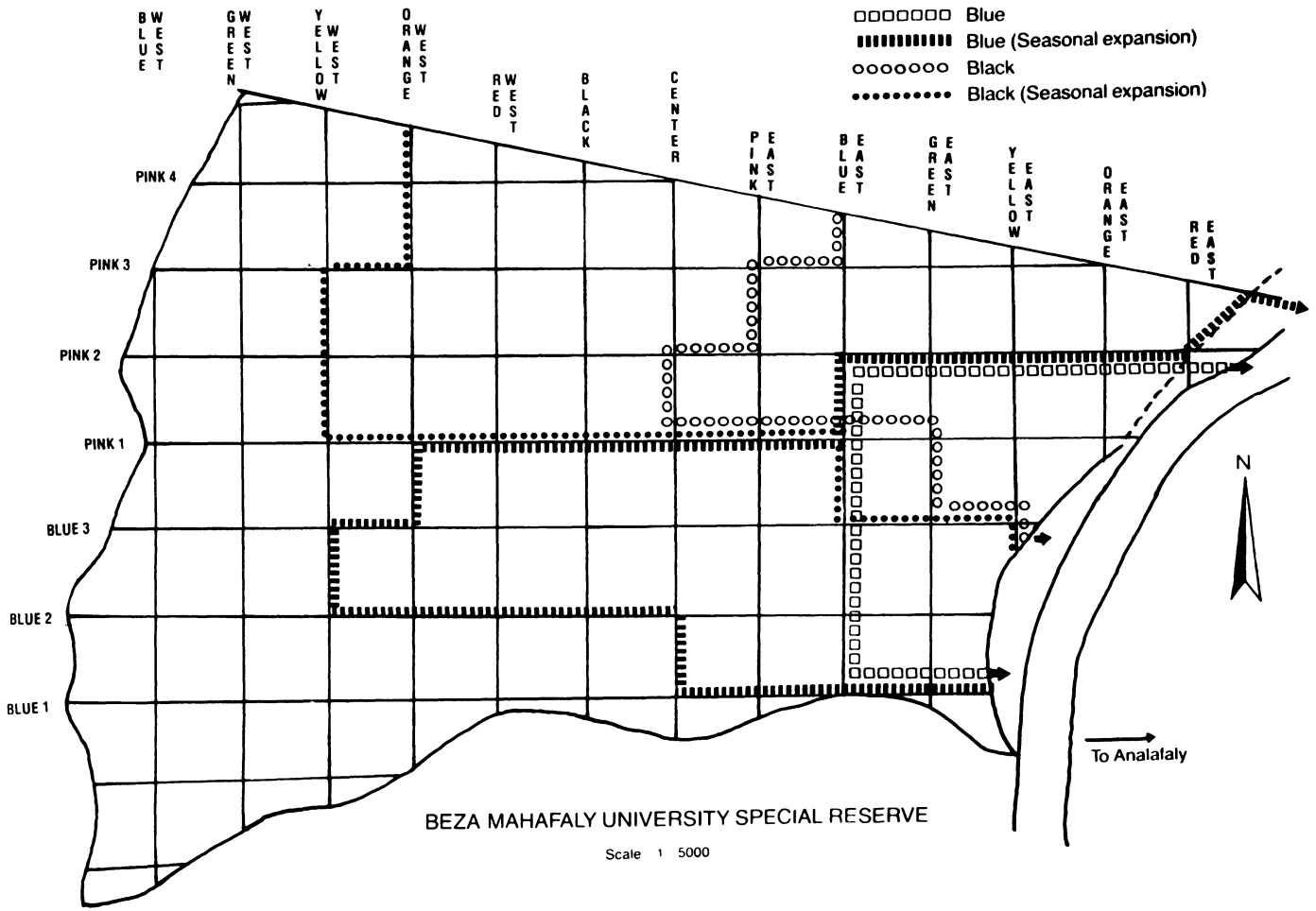

Figure 1. Map Showing Seasonal Home Range Expansion During October and November for Two Groups at Beza Mahafaly Reserve.

results of intergroup encounters between ringtailed lemurs at Beza Mahafaly during a 13 month period. The percentage of wins are based on where the encounter occurred. Of the 58 intergroup encounters the majority of wins (57%), occurred within the winner's most intensively (but not exclusively) used portion of their own home range. "Draws" (28%), where neither troop wins (i.e., feeds at the contested site), most often occurred in less commonly used areas. Group size had little effect on the outcome of such encounters. Larger troops only won when the groups fought in equally used portions of the ranges.

Table 1. Results of intergroup encounters between ringtailed lemurs at Beza Mahafaly.

Location	Result of Intergroup Encounters (N=58)	
	Win	Draw
Own Home Range	57%	0
Another Troop's Home Range	5%	0
Area Where Home Ranges Overlap:		28%
Bigger Group	9%	0
Smaller Group	1%	0

Social Organization

Spatial Relationships of Individuals Within Groups. By social organization, we refer to the pattern of social interactions which occur between individuals and between groups. Like many cercopithecine monkeys, *Lemur catta* lives in multi-male, female resident groups in which females remain in their natal group and males migrate (Sussman, 1992). Groups are centered around a core of adult females and their offspring. Furthermore, females are organized along matrilineal kinship lines with more friendly social interactions occurring between close relatives and more serious aggressive encounters taking place between nonrelatives (Taylor and Sussman, 1985; Taylor, 1986).

Males regularly migrate into and out of the marked study population. We assume many missing males have moved into unmarked groups (see Sussman, 1992). Males migrate from their natal group between 3 to 5 years of age. On average, mature males migrate every 3.5 years, with approximately 30% migrating each year (Sussman, 1992). At Beza Mahafaly, after 6 years (between 1987 and 1992) only 7 adult males out of 43 (16%) are still in their original group, and only 14 originally tagged males (33%) are still in the census population (as opposed to 62% of the originally tagged females, all of which are in their original group).

For the Beza Mahafaly groups, there are a number of males which can be differentiated by their closeness to the central core of females and by a higher percentage of friendly interactions with group females. These include lower-ranking, adult-sized natal males (3-year olds) who are often found in close association with their mothers. One or more non-natal "central males" are also found in this core group. Among these males, there is one agonistically dominant male that has feeding and mating priority over other males. In all groups studied at Beza Mahafaly, the dominant male has been in the prime adult age category (see Sussman, 1991). Peripheral males are not a cohesive subgroup but include lower-ranking males and males attempting to migrate into the group. The latter are the most peripheralized animals and are challenged by other group members of both sexes for many months.

Dominance Relationships. There are dominance hierarchies within both captive and free-ranging groups of *L. catta* (Taylor and Sussman, 1985; Taylor, 1986; Sauther, 1992) and ringtailed lemurs have been characterized as female dominant (Jolly, 1966; Budnitz and Dainis, 1975; Taylor, 1986). Dominance hierarchies were based on winners/losers in agonistic encounters and approach-retreat behavior, which both gave the same hierarchies. A single, top-ranking female appears to be the focal point for the rest of the troop. She often initiates the direction of group progressions, although as Jolly (1966) has pointed out, other individuals (including low-ranking adult males) may lead the actual travel.

Top-ranking males and females may leave the troop on occasions, and travel to where other troops are located. At Beza Mahafaly the importance of the top-ranking female was highlighted when on two occasions she left the troop and travelled several hundred meters alone. She was separated from her troop for 45 minutes. During this time the rest of the troop became visibly agitated, and began to frantically contact call when she disappeared. Departure of the dominant male did not elicit such behavior, nor did the temporary absence of several lower ranking females who on one occasion became separated from the rest of the troop.

Ringtailed lemur groups characteristically contain more than one matriline. For example, in the two intensively studied groups at Beza Mahafaly, two or more adult females were accompanied by one adult offspring, a juvenile and an infant. In captivity some matrilines of a single *L. catta* group are dominant to others, and if a group becomes too large one matriline may be evicted by another (Taylor and Sussman, 1985; Taylor, 1986). In several macaque species groups can fission, with low-ranking matrilines forming new groups (Chepko-Sade and Sade, 1979; Koyama, 1970). It is possible that group fission, which has been observed at Beza Mahafaly (Sussman, 1991, 1992), also may be along matrilines. Alternatively, if a matriline is too small to establish itself as a new group, it may transfer into another group. This may explain a single case of female transfer at Beza Mahafaly involving a mother-daughter pair who entered a new group (which contained only four adult females) and immediately became the two top-ranking females in the group (Kaufmann, pers. comm.). After this transfer two of the original females disappeared. In all cases of male transfer, the males hold low-ranking and peripheral positions upon entering a new group.

Among males, although there is one male who dominates all other males in priority of access to food and who has mating priority, there does not seem to be a consistent linear hierarchy (Budnitz and Dainis, 1975; Taylor, 1986; Kappeler, 1990; Sauther, 1992; L. Gould, pers. comm.). This may be because the adult male component of a group is constantly changing. For example, over a six year period, only three males have maintained their dominant position in the nine study groups at Beza Mahafaly. Furthermore, there are a number of different "types" of males in a group at any one time. A group might contain young adult natal males, young adults after their first transfer, prime adult multi-transfer males, old subordinate males, and males in the process of transferring into the group. From our preliminary data at Beza Mahafaly we suspect that the "central males" include prime adult and some natal young adult males from high status matrilines, whereas the peripheral males are mainly young first transfers, recent multi-transfer male immigrants, and older males. The fact that three males were able to maintain their dominance position for 6 years shows a pattern more similar to male rhesus macaques than to male baboons, with some macaque males maintaining alpha position within a group for 5 to 10 years (Bercovitch, 1991). Males currently attempting to immigrate into the groups are the most peripheralized animals and are challenged by both group females and males for many months. Thus, a cohesive subgroup of subordinate males, the "Drones Club" described by Jolly (1966) for the Berenty groups have not been seen at Beza Mahafaly. Although males form partnerships while transferring (Jones, 1983; Sussman, 1992), we do not know if any male-male alliances continue once group membership is attained.

Aggressive Interactions. Although Budnitz and Dainis (1975) report that males at Berenty were involved in more agonistic encounters than females, the actual percentage based on their Table 3 shows that males and females were involved in

similar percentages of agonism overall. At Beza Mahafaly, females were involved in significantly higher mean percentages of agonism than males. This held true for both feeding agonism as well as agonism over resting, sunning and drinking sites (Table 2). This suggests that not only are females dominant in this species, but that they are actively involved in a greater percentage of agonistic encounters than are males. Male aggression, on the other hand, was greater than that of females only for the month of April, just prior to the mating season in May.

Table 2. Percentage of agonism involving female and male ringtailed lemurs at Beza Mahafaly.

Green Troop	Feeding	Non-Feeding
Females	59	56
Males	41	44
Females *vs* Males	$t=7.46$; $p<0.05$*	$t=4.76$; $p<0.05$
	$N=1375$	$N=785$
Black Troop	**Feeding**	**Non-Feeding**
Females	71	64
Males	29	22
Females *vs* Males	$t=14.21$; $p<0.05$	$t=3.77$; $p<0.05$
	$N=555$	$N=98$

*Randomization procedure (see Manly, 1991; Sauther, 1993). Sample sizes were Green Troop: 5 females and 5 males; Black Troop: 4 females and 2 males.

In the two groups studied intensively at Beza Mahafaly the top-ranking female was responsible for the greatest number of aggressive encounters overall. In both troops the top-ranking female also won all such encounters. The majority of these involved access to food.

Although adult females are dominant to males, at Beza Mahafaly, in depth observations of identified individuals revealed that female dominance is gradually established, and appears to become stable after a female's first mating season. Prior to their first estrus, young females of adult body size (aged 2 years) were sometimes displaced from feeding and drinking sites by adult males (Sauther, 1992). Approximately 3% of all male-female agonistic dyads involved males displacing females. These were non-aggressive displacements. Males would simply move females out of the way with their bodies. During the mating season these females were repeatedly approached by adult males, and young, non-receptive females quickly learned that the only way to curtail such unwanted advances was to aggressively cuff or chase the male away. After the mating season these same females dramatically increased the percentage of feeding displacements directed toward males (pre- *vs* post-mating: $x=0.08\%$ *vs* 3%, $N=3$ females, 7 males, $t=2.74$, $P<0.0005$, randomization procedure). Such consistent and large increases in feeding agonism directed toward males did not occur among older adult females (pre- *vs* post-mating: $x=3.2\%$ *vs* 2.7%, $N=6$ females, 7 males, $t=0.40$, $P=0.38$, randomization procedure).

Mating Season. Jolly (1966) and Budnitz and Dainis (1975) both report that subordinate males successfully mated with troop females at Berenty during the brief mating season. While this has also been observed at Beza Mahafaly, the actual order of mating reflected the dominance hierarchy of non-natal males. In all observed cases the most dominant, central male was the first to mate and ejaculate when a female initially became receptive. The second ranked male mated next. The next individuals

to mate were transferring males and/or non-group males. Thus, the dominance hierarchy did not break down with respect to the *order* of mating for the two top ranking males (Sauther, 1991). Koyama (1988) observed a similar pattern at Berenty, where a single high-ranking male was the first to mate with receptive females. Male rank can change, however, and in one recent case during the mating season the third ranked male moved up to the top ranking position and was then the first to mate (L. Gould., pers. comm.).

Observations during the mating season at Beza Mahafaly support other reports from captive groups (Taylor and Sussman, 1985; Taylor, 1976, Pereira and Weiss, 1991) that female mate choice is an important reproductive strategy in ringtailed lemurs. Female mate choice is defined here as a female rejecting, (i.e., cuffing, chasing away, sitting down) copulation attempts of certain males, but a female approaching and presenting to other males after the onset of her receptivity. Of the 17 matings observed during the 1988 mating season, 47% of these involved an initial approach by the female, and in spite of vigorous and persistent harassment by group males, 35% of these matings involved mating with males of other groups.

Mating Strategies. It has been recently suggested that infanticide may be an adaptive aspect of the mating system of ringtailed lemurs (Pereira and Weiss, 1991). In semi-free-ranging groups of ringtailed lemurs at the Duke University Primate Center, females have been reported to repeatedly attack and chase males attempting to immigrate during the lactation period. Such female aggression is presumed to be a response to preventing infanticide by males, which is suggested to be an established male strategy which has developed in tandem with patterns of female mate choice in this species. The rationale behind such a strategy is that it may influence female reproductive success. If a female loses her infant one year, it is suggested that her next infant has a better chance at survival. "By killing current infants, then, male lemurs may often advance by a full year the time of females' next successful reproduction...When infants die, for whatever reason, their fathers become unlikely to be chosen again as mates ("incompetent fathers")" (Pereira and Weiss, 1991, pp. 149-150).

This hypothesis is problematic on a number of levels. First, despite thousands of hours of observation on identified, habituated individuals, the phenomena of increased agonism directed by females toward males during the lactation period has not been observed in most studies of free-ranging, or semi-free-ranging populations (Taylor, 1986; Gould, 1991, 1992; Sauther, 1992; 1993, Sussman unpubl. data). Furthermore, no relationship between parity or rank and agonsitic behavior by females toward migrating males has been observed. For example, from February to May, 1988 a new male (number 60) attempted to transfer into Green troop. The female showing the highest level of agonism toward this new male was number 53, who was lactating at the time. However female 13, who was also nursing, exhibited similar percentages of agonism toward this male as did non-lactating female 33. Furthermore female 93, also a non-lactating female, had the second highest percentage of agonism toward this male (Table 3).

Second, our census data indicate that 80-85% of females give birth annually, and between 30-50% of these infants perish each year. If infanticide is a viable male strategy, presumably a high proportion of these deaths should be due to *male* infanticidal activities. Recently, two instances of infant-killing have been reported at Berenty (M. Pereira, pers. comm.). Intergroup encounters and agonism between females of different groups peak during the birth season (Sauther, 1992). Because infants can be wounded and/or killed during aggressive encounters between *females* of different groups (S. O'Connor; M. Gould, pers. comm.) it is essential that such observations be made on clearly identified animals. Infanticide in ringtailed lemurs has not been observed among individually identified ringtails at Beza Mahafaly (Sussman and Sauther, unpubl. data; M. Pereira, pers. comm.). In fact, during a year of intensive observations of two groups of ringtailed lemurs at Beza Mahafaly we failed to observe a single episode of male aggression directed toward any infant. Furthermore, and perhaps most importantly, in the birth seasons between 1987 and 1990, 16 of 19 females (84%) followed for the 3 years successfully produced surviving infants (those living to one year of age) two years in a row. Six of these females (32%)

were successful in reproducing surviving infants for 3 consecutive years (Sussman, unpubl. data). As in many mammals, infant survival of ringtailed lemurs at Beza Mahafaly is related to the age of the mothers, with young prime and prime-aged females having higher infant survival rates and older females lower rates (Sussman, 1991).

Table 3. Percentage of agonism between transferring male, 60, and female members of Green troop.

Dyad	Agonism[1]	Context	
		Feed	Space
53 & 60[2]	37	34	2
93 & 60	16	11	5
33 & 60	11	3	8
13 & 60	11	8	3

[1]Agonism involving females only.
[2]Significantly greater at $p<0.05$ than all other dyads except "Space" for 93 & 60, t-test significance determined by the randomization procedure.

Third, because females regularly mate with a number of males both from within and outside of the group, it is difficult to conceive of either the female or the male recognizing the father of any particular infant, a prerequisite for the incompetant father hypothesis of Pereira and Weiss (1991). This pattern of multimale mating has been observed both at Berenty and Beza Mahafaly and is clearly a part of the female mating strategy. It is therefore difficult to understand the advantages of infanticide as a male reproductive strategy in *Lemur catta*.

We believe that an interplay between stochastic events, (predation, parasites, illness, falls) and the precocial development pattern in this species are more likely responsible for infant mortality in ringtailed lemurs. Although we agree, and have presented elsewhere (Sauther, 1991) that male mating strategies are adapted to female mate choice, we do not believe that infanticide is a viable tactic. Instead, we hypothesize that the dramatic seasonal fluctuation of resource availability in this species makes it essential for females to time their reproduction so that infants can be weaned during the period of relative food abundance (see also Martin, 1972). All females enter estrus during the same, short mating season and thus mating with more than one male helps insure fertilization during this short receptive period. This does not mean that females will mate with all males present, but rather that they will *selectively* mate with more than one male, and at least one of these mates may be from outside of the group (see also Sauther, 1991).

Female choice of multiple group and non-group males results in a number of male mating strategies (Fig. 2). One of the adaptive advantages of becoming a central male appears to be the ability of this male to establish close relationships with females throughout the year (Sauther, unpubl. data), and thus to gain first access during mating (c.f. Smuts, 1985). Becoming the female's first mating partner may be especially inportant in *L. catta* as there is evidence that mating with ejaculation may lead to a loss of receptivity (Evans and Goy, 1968; van Horn and Resko, 1977). Furthermore, Evans and Goy found that within 2 hours of the first male's ejaculation females began rejecting males and that "Subsequent males rarely achieved more than incomplete sequences with probable intromissions" (p. 188). Close relationships with group females allows the top-ranking central male to monitor the reproductive state of group females during the short breeding season and to limit sexual monitoring by other males. He also forms a consortship with females nearing estrus, thereby

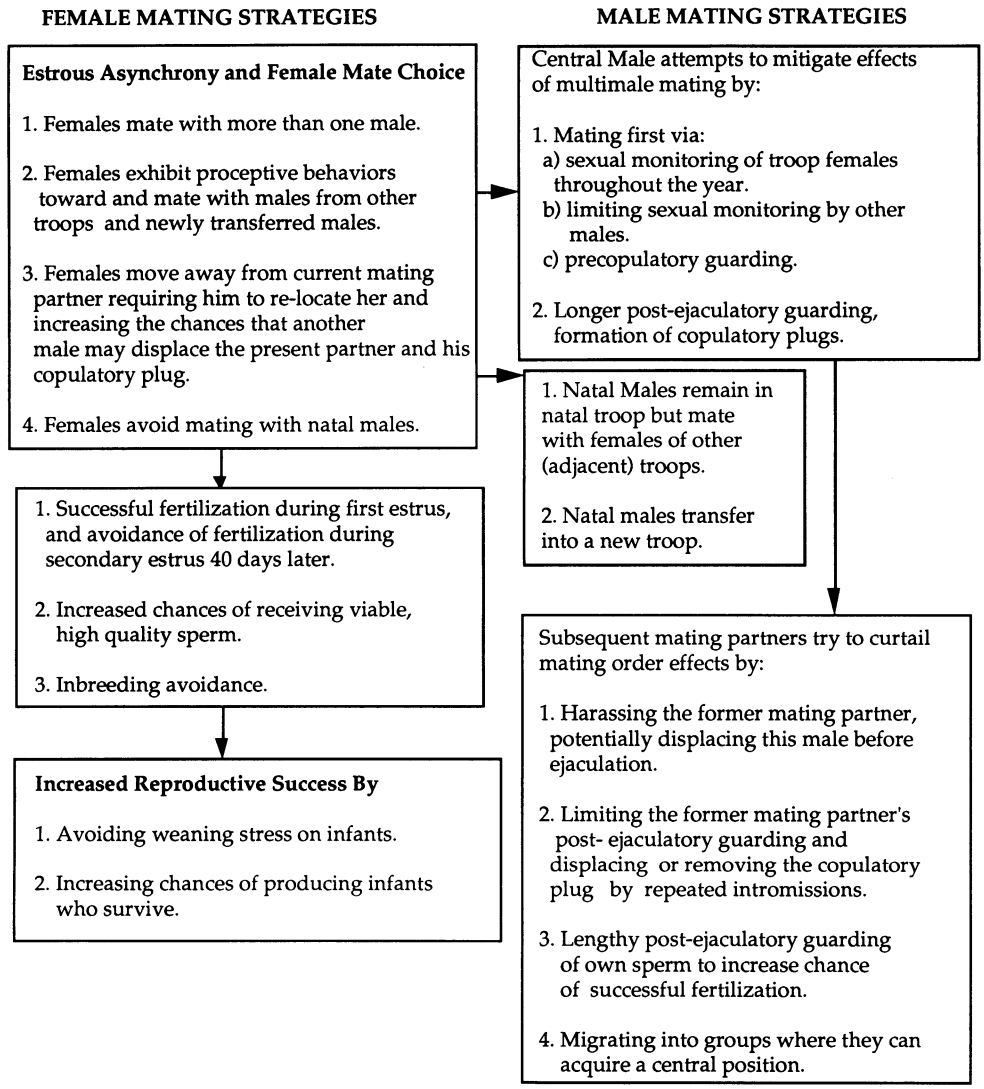

Figure 2. A model of mating strategies for ringtailed lemurs (modified from Sauther, 1991).

increasing his chance of being the first to mate if he is acceptable to the female when she becomes behaviorally receptive. The central male is also able to delay successive matings by other males, allowing the formation of a copulatory plug which might impede fertilization by other mating partners. Other males vigorously harass such males, potentially displacing them before ejaculation, or at least limiting the length of post-copulatory guarding. If successful, they attempt to replace the former mating partner as quickly as possible, which may inable them to displace previous copulatory plugs. They then guard the female for as long as possible after their ejaculation.

In any case, without evidence that these incidents do in fact lead to increased survival of the offspring of infanticidal males, the burden of proof for this hypothesis falls on its proponents. It should not be accepted as fact because it is an elegant hypothesis. Clearly further information is needed to prove or disprove either hypothesis.

ACKNOWLEDGEMENTS

We would like to thank the following people for their assistance at Beza Mahafaly: Glen Green, Jeff Kaufmann, Alison Lake, Manjagasy, Armand Rakotozafy and Katie Reilly. The project would not be possible without the generous aide of the Ministry of Higher Education and the School of Agronomy of the University of Madagascar, especially Mme Berthe Rakotosamimanana, Benjamin Andriamihaja, Joseph Andriamampianina, and Pothin Rakotomanga. The hospitality and assistance of the people of Analafaly and the reserve guards in also gratefully acknowledged. The project was funded mainly by the World Wildlife Fund, a Fulbright Senior Research Grant, a Fulbright Collaborative Grant, the National Geographic Society, the Leakey Fund, and NSF Grant #BNS-8619240.

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