

Reproductive Behavior of Free-Ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar

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ABSTRACT Observations of reproductive behavior in free-ranging *Lemur catta* were carried out during one annual cycle. Variability in the behavior of female ringtailed lemurs during parturition appears to be mainly a function of the female's parity and thus her experience. Females within a troop show estrous asynchrony and characteristically mate with more than one male. Females also exhibit proceptive behavior toward and mate with some males from other troops and with transferring males. The potential for a male to monopolize mating opportunities during a female's short estrous period is therefore limited. Male mating strategies in ringtailed lemurs can be seen as adaptations to female mate choice during a highly restricted breeding season. In this species the dominance hierarchy does not break down with regard to the order of mating. The highest ranking male (central male) mates first and shows precopulatory guarding and longer postejaculatory guarding, which may increase his chances of siring the offspring. Subsequent mating partners have developed various counterstrategies to mitigate mating order effects.

There are few published accounts of reproductive behavior in wild prosimians. General aspects of reproductive behavior in *Lemur catta* have been reported (Jolly, 1966; Budnitz and Dainis, 1975; Mertl-Millhollen et al., 1979; Koyama, 1988), but all of these studies have been carried out at Berenty (a private reserve in southeastern Madagascar). Captive studies of ringtailed lemurs have provided information on *L. catta* reproductive biology and behavior (Evans and Goy, 1968; Van Horn and Eaton, 1979; Van Horn, 1980) but cannot give the natural contexts for such behavior. This intensive study of individually tagged and collared ringtailed lemurs at the Beza Mahafaly Special Reserve, Madagascar, describes the reproductive behavior of known individuals during one annual cycle. Female and male mating behavior and female behavior during parturition is described, and a model of *L. catta* mating strategies is presented.

MATERIALS AND METHODS

Study site

Research was conducted at the Beza Mahafaly Special Reserve, which is located ap-

proximately 35 km northeast of the town of Betioky (23°30'S lat., 44°40'E long.). 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; see also Sauther, 1989).

The 13 month study (October, 1987, to November, 1988) concentrated on ringtailed lemurs living within an 80 ha fenced and guarded portion of the reserve. The area contains a deciduous and semideciduous riverine forest, which becomes more xerophytic as one moves from the east to the west. It is dominated by *Tamarindus indica* in the east, which becomes codominant with *Salva-*

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dora augustifolia and *Euphorbia tirucalli* in the west. Grazing by sheep and cattle is prohibited, and a rich understory of herbs and lianas is present. The habitat is seasonal, with a hot/wet season and a cool/dry season. Based on daily records of temperature and precipitation, the mean high for the austral summer at the reserve (October–March) is 37°C, but temperatures can reach 46°C. The mean low during the austral summer is 22°C. The mean high during the austral winter (April–September) is 32°C, and the mean low is 14°C. Total annual precipitation is 522 mm, with 506 mm falling during the austral summer, and rain falling on 47 days.

Study subjects

Nine troops of ringtailed lemurs range within the study area. As a part of a long-term demographic study by R.W. Sussman, all adult females, most adult males and most subadult 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 interindividual variability in the feeding ecology of two *L. catta* troops (Black Troop and Green Troop). Members of these troops are described in Table 1. Two adult males in Green Troop and two males in adjacent Blue Troop were natal males; they had been previously tagged and/or collared as juveniles. Focal animals were sampled at 5 min intervals (Altmann, 1974), and data were entered directly into handheld portable computers (Tandy 102) powered by solar-rechargeable batteries. Data were stored on 3.5 inch computer diskettes. The behavior of each adult member was sampled 1 day per month for at least 7 hr. Continuous daily observations of both troops by myself and a research assistant were made during the mating season (the month of May) and during the birth season (from late September through early November). Troops were habituated to observers, allowing close range observations (1–2 m). A total of 16 *L. catta* (seven males and nine females) were studied, and over 1800 hr of observations were collected. Opportunistic observations of adjacent troops (Red Troop and Blue Troop) were also made.

Definition of terms

Receptivity refers to females who are willing to copulate with certain males, and *pro-*

ceptivity applies to females who approach and hindquarter present to males. Neither term implies equal and indiscriminate acceptance of all males. *Behavioral estrus* refers to females showing receptive and/or proceptive behavior. *Female mate choice* is defined as a female rejecting (i.e., cuffing, chasing away, sitting down) copulation attempts of certain males but initiating or accepting copulation with other males after the onset of her receptivity. Females not in behavioral estrus also rejected male mating attempts by cuffing. Therefore, rejections were referred to as *female mate choice* only if the female had previously presented to and mated with another male. *Postejaculatory guarding* refers to the male's attempt to block sexual advances from other males after he has ejaculated. This involved chasing and/or fighting males who tried to approach the estrous female.

Observations of female mating behavior were made on six females, three from Green Troop and three from Black Troop. All these females were multiparous. For three other nulliparous females, two from Green Troop and one from Black Troop, actual mating was not observed. Each of these females did exhibit a copulatory "plug" (made of hardened ejaculate) and subsequently gave birth. These females were 2.5 years old and were mating for the first time. Successful matings (to ejaculation) were observed for seven males.

Gestation lengths were calculated from the day a female was observed mating (six females) or the first appearance of the copulatory plug (three females) to the birth of the infant. Captive studies indicate that, although the copulatory plug forms within minutes in the vaginal canal, these plugs are not visible until 1–2 days after mating (Evans and Goy, 1968). Continuous daily observations of both troops were made during the birth season, and each morning all females were checked for the presence of a new infant.

Observational conditions of labor were excellent, and it was possible to divide labor into four stages following Bowden et al. (1967). Stage one begins with the onset of observable uterine contractions, includes the rupture of the amniotic sac, and ends with "crowning" (the first appearance of the infant's head; Trevathan, 1987). Stage two starts with the appearance of the fetus' head and ends when it is expelled from the uterus. Stage three is from delivery of the neonate to

TABLE 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 ²	3	TNT ³	
	86 ²	4		
	70 ⁴			
	60 ⁵ 23 ⁶			
Juveniles ⁷	One female One male		one male	
Infants	One female (born 10/87)		One female (born 10/87)	
	One male (born 10/87)		One male (born 10/87)	

¹Central male.

²Natal males, each 2.5 years old. These males were initially collared and tagged at age 18 months by R.W. Sussman.

³A 3.5-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.

⁴Peripheral male of Green Troop. No agonistic episodes were recorded between this male and males 86 or 50. This male did clearly rank below 10 and 30, however.

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

⁶A 3.5-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.

⁷All juveniles were 18 months old.

the expulsion of the placenta, and stage four is the time taken to eat the placenta.

Social status was determined for all adult members using three measures: approach/retreat, displacement, and winner/loser in agonistic encounters. All three measures yielded the same stable hierarchies for all adult individuals. The highest ranking male is referred to as the *central male*; he 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). *Peripheral males* were males who rarely interacted with core females and who were normally some distance away from them.

RESULTS

Precopulatory and copulatory behavior

Matings in Green Troop and Black Troop showed a distinctly seasonal pattern. The mating season lasted 9 days for Black Troop and 20 days for Green Troop. All observed matings, including one in Blue Troop and one in Red Troop, occurred during a 20 day period in May. Females within each troop showed mating asynchrony; each female was in behavioral estrus on separate days. Two females came into behavioral estrus in the morning, and four females first became re-

ceptive in the afternoon. Females were in behavioral estrus for at least 6 hr but for no longer than 24 hr.

Approximately 1 week before behavioral estrus, the females' vulvae increased in size and the vaginal orifice became flushed and red. Interindividual variation occurred, with changes in vulva size being most dramatic in the alpha female of each troop. Nulliparous females who were undergoing their first estrus showed the least change. By the day after mating, the vulvae had visibly decreased in size. Within 2 days they were back to normal size and coloration.

Whereas female *L. catta* exhibited behavioral estrus for no more than 24 hr per year, erections in male *L. catta* not associated with actual mating (n = 54) were observed throughout the year (Fig. 1). There was a gradual increase in erections beginning in February. Erections reached a peak during May, when all observed matings took place. Another increase occurred during the birth season, with a second peak in October.

Males would periodically monitor a female's reproductive state by approaching her, "tail marking" (embedding the tail with glandular secretions from the brachial and antibrachial glands), "tail waving" (flicking his tail at her), and attempting to smell or

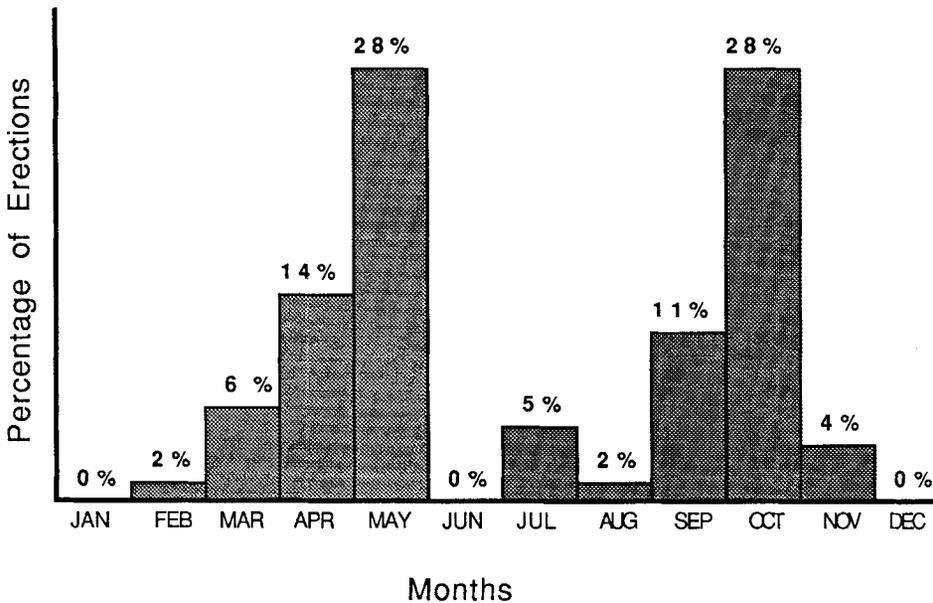


Fig. 1. Percentages of erections by month in *Lemur catta* males at Beza Mahafaly Special Reserve.

lick her genitals. Males monitored multiparous females' reproductive state throughout the year. These sexual approaches reached a peak during the mating season in May and then abruptly declined (Fig. 2). There was also a second, smaller peak just prior to the birth season. Beginning in April, males would also smell areas just vacated by females.

In both troops, the central male engaged in precopulatory guarding. Central males curtailed close contact between females nearing estrus and other males by "stink fights" (Jolly, 1966) and by agonistic displacement of the males. This limited monitoring by other males. Central males also maintained closer proximity to females during May than did other males. They would approach, sit near, and even rest/sleep in contact with females during the midday rests. Therefore, they were nearest when receptivity occurred. This behavior was exhibited only toward females who had not yet mated and began 1-2 days before the female became receptive.

All multiparous females not in behavioral estrus would react to male monitoring by either cuffing or chasing him away. Nulliparous females were approached by monitoring males beginning in February. They ap-

peared at first uncertain of how to respond to such male attention, and initially they gave only light cuffs. However, ignoring male advances resulted in mounting attempts by the male, and these females quickly began to react with heavy cuffs or chases. By the end of the mating season, the responses of nulliparous females to male monitoring were indistinguishable from those of multiparous females.

The onset of receptivity was clearly defined for multiparous ringtailed females. If the female was in behavioral estrus and if the male was acceptable to her, she either allowed the male to approach and mount her or actively presented to the male by approaching him, orienting her backside toward him, raising her tail, and looking over her shoulder at him. For all observed matings, we were present at the initial onset of behavioral estrus. However, there were no clear signs of when this might occur. For example, female 53 of Green Troop rebuffed the advances of the central male (10) at 1630 hr, but 30 min later she approached and presented to him and they mated.

Only adult males, aged 3 years or older, were observed to mate. Although the 2.5-year-old natal males of Green Troop (86 and 50) showed the full complement of adult

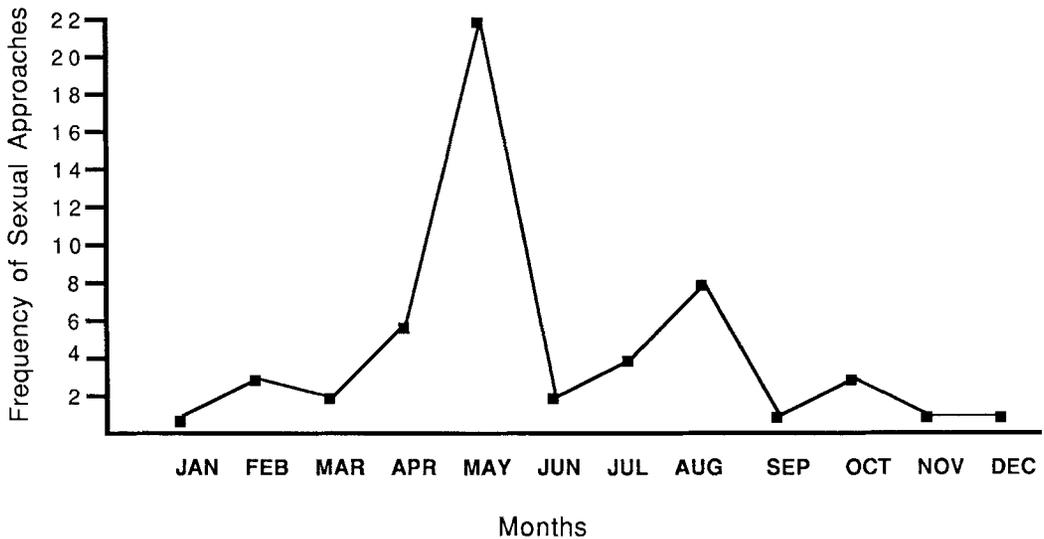


Fig. 2. Male *Lemur catta* sexual monitoring of female *Lemur catta* at Beza Mahafaly Special Reserve.

male behavior (sexually approaching estrous females, exhibiting erections, howling, and chasing nontroop males), they were not observed to mate. This was due to rejection by some troop females and to the natal males' inability to usurp the female's current mating partner (see Discussion). By the 1989 census, both these males had transferred out of their natal troop. In addition, the most peripheral troop male of Green Troop (70) was never observed copulating. Although he sexually approached females, he was unable to displace the female's current mating partner. This male eventually transferred with male 60 into nearby Blue Troop, but, by the 1989 census, he had disappeared from the reserve.

The three nulliparous females were not observed copulating; however, all three developed copulatory plugs. This suggests that mating occurred either after dark or before dawn, since these females were being closely watched throughout the day. While the central male spent most of his time sitting near and monitoring each of the nulliparous females 2 days before the mating plugs appeared, by the next day he totally ignored these same females, as did all other males, suggesting that mating had occurred at night. Copulatory plugs appeared within 1–2 days of estimated mating and lasted for 1 day. Females were visibly bothered by the

presence of these plugs, which they licked and chewed at.

Female ringtailed lemurs did not copulate with all males during receptivity (Table 2). Sexual approaches by natal males were rejected by some females, who would cuff them, chase them, or simply sit down, yet these same females did mate with other adult males. Furthermore, despite persistent harassment by troop males, females approached, presented to, and mated with transferring males and with some males from adjacent troops.

Female mate choice also affected the order of mating. In Black Troop, female 82 began her mating bouts with the central male (99) of her group. When this male briefly left her to chase away the other troop male, a male from an adjacent troop (TNT) approached her, at which time 82 cuffed him away. However, after 82 had mated with the central male and the other troop male, she then actively sought out, presented to, and mated with TNT despite attempted interruptions by the two adult troop males and the juvenile male. Similarly, female 53 of Green Troop unambiguously approached and presented to her troop's central male when she first became behaviorally receptive.

The actual order of mating reflected the dominance hierarchy of nonnatal males. In all observed cases the central male in both

TABLE 2. Mate choice during receptivity by female Lemur catta at Beza Mahafaly Special Reserve

Female	Presents to	Accepts	Rejects
33	60 ¹	10, 30, 23 ²	86, ³ 50 ⁴
13	60	10, 30	86, 50
53	10 ⁵		
82	TNT ⁶	99, 19	JU, ⁷ IN ⁸
42	TNT	99, 19	
02		99, 19, TNT	

¹Transferring male.

²Male from Blue Troop.

³Son of female 33.

⁴Natal male of Green Troop.

⁵Proceptive behavior toward central male. Other males approached her, but only the central male was observed to mate before darkness curtailed observations.

⁶Male from Blue Troop. He was rejected by 82 until female mated with all adult troop males.

⁷Eighteen-month-old juvenile sexually monitored and attempted to mount his sister.

⁸Six-month-old male infant attempted to mount his mother.

troops was the first to mate and ejaculate when a female initially became receptive (Table 3). The second-ranked male mated next; then the transfer and/or nontroop males mated. These were not peaceful progressions. In all cases, more than one male would approach a receptive female, and aggressive fights often occurred. On one occasion two males fighting in a tree over a receptive female fell 8 m into dense brush, only to climb the tree rapidly once more. "Jump fights" (Jolly, 1966) also occurred, and sightings of males with deep wounds were commonplace during the mating season.

Mating usually involved an initial approach by the male. In five cases, however, females approached and presented to the male (Table 2). One female approached the central male (10), two females approached a transferring male (60), and two other females approached the same male (TNT) from an adjacent troop after these females had already mated with troop males.

Although matings were observed at all levels of the forest, they tended to occur at lower levels, 2–3 m high, or on fallen branches on the ground. A mating bout began with a number of short mounts without intromission. Usually the male mounted and then quickly dismounted to chase away other approaching males. These chases were protracted and vigorous and involved leaps into bushes and climbing up and down trees. Females often moved off during these chases, which required her current mating partner to relocate her. During this time a male could mount, with or without intromis-

sion and thrusting, for as many as 25 times before ejaculation. These mounts were very short in duration, averaging about 21 seconds.

After a series of brief mounts, there was a long mount with intromission, with a mean length of 1 min 34 sec ($n = 11$, range 1.04–2.05 min). This mount involved several deep thrusts and a long hold, and then the male would dismount. Only after this bout could ejaculate be seen on the penis, which the male would then lick. Each male was observed ejaculating only once during his mating bout with any one female. The female continued to present to the male, and in two cases the male briefly mounted the female again within 30 sec of the ejaculatory mount. After all other ejaculatory mounts the male ceased mounting and instead focused on guarding the female from other males. Postejaculatory guarding was observed after all but one mating bout (with nontroop male 23). Central males had longer bouts of postejaculatory guarding, whereas nontroop males had the shortest bouts (Table 3). The sequence would be repeated when a new male displaced the female's previous mating partner. Once a male had lost access to a female, he might continue to "harass" the new mating partner, or simply lose interest, but he was never again observed attempting to mate with that female, and she never again presented to him.

Two mating bouts with separate females in Black Troop were unusual. They both involved the same male (TNT), who resided in a nearby Blue Troop and had been shadowing Black Troop since late April. In both cases large amounts of blood were observed on the male's penis and the female's vulva near the end of the mating bout. The source of the blood was not obvious.

There was a striking decrease in male weight and general appearance by the end of the mating season. In April all males appeared heavy and had fine, healthy coats. By the end of the mating season, these same males had visibly lost weight and had dull coats. Females appeared to be under nutritional stress during the last part of lactation (February–March). During this period they were thin and had dull coats. Once the infants were weaned, females rapidly gained weight and were in good condition by the mating season. Unlike the males, they retained this healthy appearance throughout the mating season and into June.

TABLE 3. Male Lemur catta mating bouts at Beza Mahafaly Special Reserve¹

Male	Social status	Female	Mating order	Number of ejaculations	Length ejaculatory bout (min)	Length of postejaculatory guarding (min)
Green Troop						
10	1	53 ²	1	1	2.05	30
10	1	13	1	1	ND	30
30	2	13	2	1	1.51	20
60	TM	13	3	1	1.50	ND
10	1	33	1	ND	ND	ND
30	2	33	2	ND	ND	ND
60	TM	33	3	ND	ND	ND
23	AT	33	4	1	1.25	0
Black Troop						
99	1	82	1	1	1.25	30
19	2	82	2	1	1.25	11
TNT	AT	82	3	1	1.23	4
99	1	42	1	1	1.11	62
19	2	42	2	1	1.24	50
TNT	AT	42	3	1	1.04	7
99	1	02	1	ND	ND	ND
19	2	02	2	ND	ND	ND
TNT	AT	02	3	1	1.34	ND

¹AT, male from an adjacent troop; TM, transferring male; ND, no data; mating was observed but numbers of ejaculations, etc., were not counted in these cases due to observational difficulties.

²Female 53 came into estrus late in the day, and only one mating bout was observed before darkness curtailed observations.

Mating behavior of males from nearby troops and transferring males

The demographic aspects of *L. catta* transfer behavior at Beza are reported elsewhere (Sussman, 1991). However, behavior of three males, TNT, 23, and 60, warrant special comment. TNT (a 3.5-year-old natal male of Blue Troop) began following the adjacent Black Troop 3 weeks prior to the onset of the mating season. During these 3 weeks and the subsequent month of May, 1988, he stayed with Black Troop both day and night. He successfully mated (copulation to ejaculation) with three of this troop's females, but by the end of the mating season TNT had returned to his original troop and was still a member by the November, 1988, census. By the November, 1989, census, this male had disappeared. In January, 1988, male 23 (also a 3.5-year-old natal male of Blue Troop) began spending approximately one-half his time in adjacent Red Troop (Sussman, 1991) and the rest of his time either with his natal troop or "visiting" Green Troop females (i.e., he approached and sexually monitored these females). Male 23 successfully mated with one of the Green Troop females (33), but he remained with his original Blue Troop through the November, 1988, census. By the July, 1990, census, this male had transferred

into Green Troop. Male 60 (origin unknown) began transferring into Green Troop in January, 1988. Male 60 remained the most peripheral male, and by April, 1988, he was spending approximately one-half his time with Green Troop and one-half his time in adjacent Blue Troop. During the mating season, this male mated with two of Green Troop's females. He then took up residence in Blue Troop full time and was still in this troop by the July, 1990, census.

Lemur catta birth season at Beza

Gestation lengths ranged from 136 to 145 days, with a mean of 141 days ($n = 9$). These nine births occurred between September 18 and October 17, 1988, but births were noted up to November 13, 1988. A single birth peak occurred in October. Of the 35 adult female *L. catta* present at Beza during the 1988 birth season, 27 (77%) gave birth. Of these females, four (11%) were known to have lost their infants within 3 days of birth. One of these females was an older multiparous female, one was a young multiparous female, and two were young primiparous females. One of the females gave birth but subsequently died, and one female (3%) disappeared by the last census in November, 1988. Seven (20%) of the females were never ob-

served with an infant. These latter females may have lost their infants before they were observed, miscarried, or failed to conceive. Although four of the seven females were old (one female being edentulous except for the tooth comb), two of these older females were observed mating in May, so they were not acyclic.

Mating seasonality resulted in birth seasonality. Black Troop females mated during a 9 day period, and all these females gave birth within 14 days of each other. Green Troop had a mating season of 20 days and a birth season of 24 days. All five females from Brown Troop gave birth during a 6 day period, and the three Red Troop females had a birth season of 24 days.

Perinatal behavior

Continuous daily observations during the birth season yielded data on four live births. The other five females gave birth during the night. Approximately 10 days before labor, the female's vulvae enlarged and reddened in a manner very similar to that observed during the mating season. The genitals returned to normal within 1 day of giving birth. Three of the observed births occurred just prior to dusk, between 5:30 and 6:00 PM, and one gave birth at 8:30 AM. None of the births was on the same day as another. All births were arboreal, and all females were alone during parturition, although the rest of the troop was within 50 m. In three cases, this was the result of the rest of the troop moving off in search of food. The alpha female, however, moved away from her troop to give birth (see below).

The stages of labor for *L. catta* are given in Table 4. The length of stage one varied greatly. One young primiparous female (73) had no observable contractions, whereas an older female (33) had 22 contractions lasting 73 min. Much of this variation seemed related to the size of the neonate. The primiparous female, 73, gave birth to a very small infant, whereas females 13, 53, and 33 had larger infants. Female 33, who had the longest labor and the largest neonate, clearly showed distress during parturition, laying on her side between contractions and making sharp little cries during the contractions just prior to birth. No other female made such vocalizations.

Contractions were visible and began with a lifting of the tail in a manner similar to defecation, a stiffening and stretching of the

body, and then relaxation. Females having contractions would periodically stand bipedally, arching the back, stretching out their bodies, and usually grasping a branch overhead. They would then crouch or lie on their side between contractions.

Once the head of the infant appeared, the three multiparous females crouched in a sitting posture, actively grasped their infant as it emerged, and pulled the neonate onto their ventrum. The primiparous female delivered the neonate standing bipedally, which resulted in the infant holding onto the base of its mother's tail, and the female holding onto her infant by its head. She was eventually able to bring the infant onto her ventrum. In ringtailed lemur births, as in most nonhuman primate births (Trevathan, 1987), the fetus was born occiput posterior. All females immediately licked mucus from the infant's face and body. Once the placenta was delivered, it was quickly eaten. The females also tugged on and ingested the umbilical cord still attached to the infant. One of the females (53) resumed feeding 15–20 min after delivery, whereas the three other females (73, 33, and 13) rested. Three of the females had to relocate their troop after parturition, but in the case of the alpha female the troop located and rejoined her (see below).

The behavior of Green Troop's alpha female (13) during labor was different from that of the three other observed births. This female left her troop 50 m away and moved to an area where she frequently genital marked small vertical tree trunks. She repeatedly moved into a series of trees and appeared to be searching for a birth site. Her troop was initially agitated at her departure, and members vocalized frequently. The central male (10) appeared, came within 10 m of her, and then returned to the rest of the troop. During this period the alpha female climbed to a crook of a tree and then twice made a "howling" (Jolly, 1966) vocalization, which has never been clearly observed in female *L. catta*. No other female was observed to give this standard male *L. catta* vocalization. Her troop did not approach her until after her infant had been delivered. The alpha female then descended to the ground and rejoined the rest of the troop as they rested. At that time the central male wrist marked the area with the spurs and glands located on the wrist. The alpha female was observed to lick the hair away from her right nipple and pull on it twice with her mouth. She then

TABLE 4. Lemur catta births at Beza Mahafaly Special Reserve

Female	Time (hr)	Contractions	Stage one ¹ (min)	Stage two ² (min)	Stage three ³ (min)	Stage four ⁴ (min)	Total labor (min)
73 ⁵	1744	0	0.00	0.10	1	10	11.10 (stage 2-4)
53	1740	13	14.36	0.20	N.D. ⁶	N.D.	14.56 (stage 1-2)
13	0830	29	38.00	2.29	6	8	46.29
33	1725	22	73.00	2.00	9	5	84.00

¹Onset of uterine contractions to rupture of amniotic sac and crowning.

²Crowning to delivery of infant.

³Delivery of infant to expulsion of placenta.

⁴Total time taken to eat the placenta.

⁵Nulliparous female. All other females were multiparous.

⁶No data. The female moved off to rejoin the rest of the troop, and expulsion and ingestion of the placenta were not observed.

reached around to her infant, who was on her back, and pulled it to her nipple, at which time the infant was first observed to nurse. She was seen manipulating her nipples in this manner on two other occasions.

Maternal behavior in the weeks just following birth differed between multiparous and primiparous mothers. Whereas all females actively groomed and nursed their infants, primiparous females were continually adjusting their former behavior to the needs of their new infants. For example, 93 of Green Troop had preferred stretching out on her stomach during midday rests but eventually altered this position only after repeated sharp cries by her clearly uncomfortable infant. Between the second and third weeks of life, infants begin environmental exploration, such as hopping off their mothers and independent climbing. On several occasions during feeding bouts, primiparous females seemingly "forgot" about their infants and moved off in search of food. The response of the infant was to utter sharp little peeps, which brought the mother (who was sometimes in the next tree) back to retrieve her infant. Such behavior was never observed in multiparous females.

DISCUSSION AND CONCLUSIONS

Estrous cycles and the length of the mating season

Polyestrus has important consequences for determining the mating season in free-ranging ringtailed lemurs. At Berenty, in 1982, all observed matings occurred within a 53 day period (Koyama, 1988). At Beza, all births occurred between September 18 and November 13, 1988. A mean gestation length

of 141 days would put all of these matings between May 1 and June 26. At Beza, this implies a mating period of about 57 days.

It is possible that, rather than representing one long season, these data represent a breeding peak during which most females in the area became impregnated and a second estrous cycle during which females who did not conceive in May were impregnated. Evans and Goy (1968) first reported that captive *L. catta* are polyestrus. They showed that, if female ringtailed lemurs did not become impregnated during their first estrus, they would have two consecutive cycles at approximately 40 day intervals. Budnitz and Dainis (1975) used birth data to determine whether a second estrus occurred in free-ranging *L. catta* at Berenty. They reported that, whereas most births occurred in September, a small number of females also gave birth between October and November. They assumed that these females became pregnant during a second estrus. At Beza, females in the two study troops ($n = 9$) experienced only one estrous period, and all but two of the births in the reserve ($n = 27$) occurred within the same 38 day period (between September 18 and October 25, 1988). These latter two females gave birth 18-25 days after parturition in the other adult females in their troop. Thus the evidence strongly suggests that the majority of females conceive during a year's first estrus, and that virtually all those that fail subsequently conceive during their second cycle.

Female mating strategies

Female mate choice. During behavioral estrus, females clearly and consistently avoided repeated mating attempts by natal

males. Sexual advances were rejected by mothers and closely related females (Table 2). In a study of semifree-ranging *L. catta* at the Duke Primate Center, Taylor and Sussman (1985) reported that all mating attempts between adult natal females and a brother and potentially related males were met with resistance by the females, who cuffed or bit the male or assumed postures that prevented intromission. Recent work by Pereira and Weiss (in press) using DNA fingerprint analysis has shown that, in semifree-ranging ringtailed lemurs, females avoided mating with close matrilineal kin. Similar behavior has been noted for several free-ranging anthropoid species (rhesus macaques: McMillan, 1982; chimpanzees: Pusey, 1980) and nonprimate species (black tailed prairie dogs: Hoogland, 1982).

In this study female mate choice affected mating order and also ensured that most females mated with more than one male and that at least one of these males was either from another troop or a transferring male (Table 2). Females showed proceptive behaviors toward some males from other troops and successfully copulated to ejaculation with them in spite of vigorous harassment by troop males. Partner preferences have also been observed in captive *L. catta* females by Van Horn and Resko (1977). They serially presented solitarily caged females with individual males and found that seven of the 12 females failed to copulate with one or more males during the female's receptive period.

Estrous asynchrony and multimale matings in L. catta. Data from both Beza and Berenty indicate that matings within any one ringtailed lemur troop are highly seasonal (Table 5). However, female ringtailed lemurs within the same troop show estrous asynchrony, with each female coming into estrus on separate days (Jolly, 1966; Koyama, 1988; this study). Using these field data and data on semifree-ranging ringtailed lemurs, Pereira (in press) has shown that estrous asynchrony in these populations of *L. catta* is unlikely to have occurred by chance alone. Females thus have the potential to mate with many males and multimale matings appear to be the norm for other wild populations of *L. catta* (Table 5). Multimale matings in ringtailed lemurs may be especially advantageous for a species with such a highly restricted mating season. Infant mortality in wild ringtailed lemurs is high (Sussman, 1991). 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 (Sauther, in preparation). Late births will occur if females are fertilized during the second estrous cycle, 40 days later. This can result in early weaning or weaning during food scarcity, which creates undue stress on the infant (Sauther, personal observation). 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.

The mating pattern in male L. catta

There were a number of similarities between the mating season and the birth season. Both were periods of increased male activity, when marking behavior, bouts of agonistic interactions, incidence of erections, and sexual monitoring all increased. This surge of activity around the birth season has been reported at Berenty (Budnitz and Dainis, 1975). In addition, at Berenty, howling vocalizations have been reported to peak during the mating season (Mertl-Millhollen et al., 1979) and at the end of the birth season (Budnitz and Dainis, 1975). Increased male activity during this period may be related to the onset of male transfer, which appears to begin around the birth season at Beza and Berenty.

Natal males have limited sexual access to troop females. At Beza, related and potentially related females rebuffed all mating attempts, and, even when sexual approaches were not rejected (e.g., female 53), these males were unable to displace the current mating partner. Similar restrictions at Berenty may also apply. Budnitz and Dainis (1975) report only two cases in which a 2.5-year-old natal male was able to mount estrous females, and this occurred when other males were preoccupied with fighting each other. In only one of the cases was the male able to mate to ejaculation. Thus, at Beza, although 2.5-year-old females successfully mated and later gave birth, natal males of this age were not observed to mate because of constraints imposed by other troop members. Natal male status does not necessarily mean reproductive isolation, however. Older natal males can establish mating relationships with females of other troops (e.g., male 23 and TNT).

Observations of mating and transfer behavior in individually identified *L. catta*

TABLE 5. Mating season and mean number of mating partners for female Lemur catta at Beza and Berenty Reserves

	Beza		Berenty ¹	
	Green Troop	Black Troop	Troop D ²	Troop A ³
Mating season	20 days (5) ⁴	9 days (4)	11 days (9)	—
Mean mating partners	3 (3)	3 (3)	—	4 (2)

¹Jolly (1966).

²Jolly's Troop 1 is now referred to as Troop D (Mertl-Millhollen et al., 1979).

³Koyama (1988).

⁴Numbers in parentheses denote number of females.

males at Beza indicate more variability and complexity than has been previously reported (Mertl-Millhollen et al., 1979; Jones, 1983). At Berenty, both Mertl-Millhollen et al. and Jones noted that males were unable to mate successfully outside of their troops. However, at Beza, males were able to mate with females of adjacent troops.

Furthermore, male transfer in ringtailed lemurs is a dynamic process that involves numerous patterns. At least three patterns can be identified in the months prior to and during the mating season. The first involves transferring males (e.g., male 60). Several months before the mating season, these males may focus on one troop or divide their time between two adjacent troops, mate in both, and then finally transfer into one of them. In the second pattern, a single male makes numerous "visits" to an adjacent troop (e.g., male 23), where he approaches and attempts to monitor females. The third pattern involves a mating season transfer (e.g., male TNT) where the male remains with a new troop only during the mating season. In the second and third patterns, males initially return to their original troops, but, in the former case, the male may eventually transfer into the adjacent troop. Both patterns could increase a male's chance to mate successfully in a new troop and may also determine the level of resistance by members of a target troop prior to actual transfer.

At Beza, males ejaculated only once with each of their mates. Koyama (1988) observed the mating behavior of six males at Berenty Reserve. He reported that one male was able to ejaculate an average of six times in 33 min. It is unclear whether Koyama differentiated ejaculations from multiple mounts. As already noted, males can and do mount with intromissions and thrusting many times before actual ejaculation, but, at Beza, they

ejaculated only once. The ejaculatory bout differed from nonejaculatory bouts in the length of the mount, the pattern of thrusting, the long hold, and the subsequent autogrooming of the genitals. This same pattern has been observed for captive ringtailed lemurs (Evans and Goy, 1968). It is unlikely that multiple ejaculations commonly occur unless a male and a female are able to move off by themselves and are not rediscovered by other males. Although Jolly (1966) noted this for one mating pair, it was not seen at Beza.

Male mating strategies

Male mating strategies in ringtailed lemurs may be adaptations to female mate choice during a highly restricted breeding season. Because females show estrous asynchrony, a single male could potentially monopolize all troop females during their behavioral estrus. However, females avoid mating with some males and seek out copulations with certain troop males and with males from nearby troops and transferring males. This limits the potential for a male to monopolize mating opportunities during a female's short estrous period. Under such conditions, morphological and behavioral adaptations to increase male reproductive success can be expected.

Behavior of the central male. The behavior of central males during the mating season may increase their chances of siring offspring. Mating behavior in *L. catta* has been characterized as socially chaotic, with the male dominance hierarchy breaking down, and all troop males having sexual access to all troop females (Jolly, 1966; Budnitz and Dainis, 1975). However, males do exhibit a social hierarchy, which is maintained throughout the rest of the year (Jolly, 1966; Sauther, in preparation), and the function of this hierarchy has been puzzling.

Mating behavior observed at Beza indicates that the dominance hierarchy does not break down with respect to the order of mating. In all observed cases, mating order mirrored the male's social status, with each troop's central male mating first.

The central male was able to mate first for a number of reasons, some of which may be interrelated. Central males exhibited precopulatory guarding, staying close to a female nearing behavioral receptivity and curtailing sexual monitoring by other troop males by means of ritualized "stink fights" (Jolly, 1966). Central males also maintained a closer proximity to females throughout the year and engaged in more affiliative activities (grooming, resting in contact) with troop females than did other males (Sauther, in preparation). Similar behavior in ringtailed lemurs was observed by Koyama (1988) at Berenty. Koyama, who observed the mating behavior in one troop of *L. catta*, reported that the top-ranked male (a recent transfer male) was not observed copulating with any female, whereas the second-ranked male was always the first mating partner. Koyama unfortunately established his dominance hierarchy during the mating season. As Jolly (1966) has noted, the normal dominance hierarchy, based on agonistic encounters, does not hold during the mating season. It is probable that the second-ranked male was in fact the central male. Koyama describes this male as "the only adult male who could rest and huddle with adult females" (p. 172); he was the male who usually made the howling vocalizations at dusk and the first male to mate with receptive females. All these behaviors are strikingly similar to the behavior of central males at Beza.

Due to the seasonal nature of mating in this species, it is critical that males establish when estrus occurs. Close contact with troop females throughout the year allows the central male to monitor their sexual state and may help determine when to begin precopulatory guarding. Analogous behavior has been reported in the golden hamster (*Mesocricetus auratus*). Huck et al. (1986) observed that the alpha male hamster often slept with a female nearing estrus, thereby increasing his chances of being the estrous female's first mating partner. In this species, there is a first male mate advantage with respect to litter composition (Huck et al., 1985). Research on semifree-ranging ringtailed lemurs at the Duke Primate Center in

Durham, North Carolina, suggests a similar advantage in ringtailed lemurs. Using complementary DNA fingerprinting analyses, Pereira and Weiss (in press) found that, in cases when more than one male mated with the estrous female (copulation to ejaculation), the female's first mate sired the offspring.

Postejaculatory guarding, copulatory plugs, and penile morphology. Males at Beza were apparently unable to remain the female's mate long enough to achieve a second ejaculation. Instead they focused on delaying subsequent ejaculations by other males. Postejaculatory guarding was observed after all but one ejaculatory bout, and troop males exhibited longer guarding than nontroop males. Postejaculatory guarding may increase the male's chances that his sperm fertilizes the female. Because copulatory plugs are common to this species, and form within minutes in the vaginal canal (Evans and Goy, 1968), the longer a male can guard a female after ejaculation, the greater the possibility that a plug may form and block or at least impede subsequent sperm. This may also explain why males ceased to mount females after a single ejaculation, even though they continued to guard the female for up to 62 min (Table 3). Further copulations might interfere with plug formation. In a comparative study of penile morphology and testicular volume in nonhuman primates, Dixson (1987) found that these reproductive organs are more specialized in species with multimale mating systems. *L. catta* possess penile spines and a complex distal penis morphology including an enlarged glans penis (Dixon, 1987). Because male *L. catta* mating involves repeated brief intromissions, with thrusting prior to ejaculation (Evans and Goy, 1968; Koyama, 1988; this study), such morphology could facilitate displacement or break up of previously formed copulatory plugs, but little is known about this in primates (Dixson, 1987).

Gestation lengths and perinatal behavior

Previously published gestation lengths have been based on captive populations and give a range of 130–135 days ($n = 50$ females; Richard, 1986), with a mean of 135.64 days ($n = 14$ females; Van Horn and Eaton, 1979). Gestation lengths at Beza ($n = 9$ females) gives a somewhat higher mean of 141 days and a range of 136–144 days.

This is the first published report of perinatal behavior in free-ranging ringtailed lemurs. There is little comparative data available on diurnal prosimian births, but parturition in *L. catta* was similar to perinatal behavior of a captive *Propithecus verreauxi* female (Eaglen and Boskoff, 1978). This female ingested the placenta, and, like *L. catta*, she nibbled and tugged on the umbilical cord. Ingestion of the umbilical cord by the mother has also been reported in captive *L. catta* (Bloxxam and Riordan, 1974). Richard (1976) observed perinatal behavior in a wild *P. verreauxi* female and noted that this female gave birth alone, while the rest of the troop continued to forage 15 m away. Similar behavior was noted for *L. catta* females giving birth at Beza. Jolly (1966) reported seeing a female who gave the howling vocalization but doubted the identification because she was never able to repeat the observation. At Beza, two instances of howling were observed by the alpha female of Green Troop just prior to parturition. In this case, the vocalization seemed to function as a contact call to the rest of her troop who were calling and searching for her.

Birth in *L. catta* appears to be similar to parturition in anthropoids. Standing and stretching during labor have been reported for a number of anthropoid primates and may serve to increase the size of the birth canal (Trevathan, 1987). Anthropoids commonly crouch to deliver the infant (Shively and Mitchell, 1986b). Chewing on the umbilical cord has been observed in the squirrel monkey, *Saimiri sciureus* (Bowden et al., 1967). Consumption of the placenta by the mother has been reported for both prosimians and anthropoids (Shively and Mitchell, 1986a,b).

Perhaps the most important similarity to anthropoid births was the active participation of multiparous *L. catta* during and just after parturition. Nocturnal prosimians are reported to be relatively lax in their maternal behavior (i.e., the mother does not help the infant maintain contact and does not assist in the delivery of the infant; Shively and Mitchell, 1986a). The quality of maternal behavior during and after parturition in *L. catta* was more a function of the parity of the mother. Multiparous *L. catta* females actively participated in their infant's birth and exhibited appropriate maternal behavior. Primiparous females clearly were inexperienced, and it was mainly the behavior of

their infants that promoted appropriate maternal responses.

A model of L. catta mating strategies

Figure 3 provides a potential model of mating strategies in female and male ringtailed lemurs. Observations from this study indicate that in species with a highly restricted mating season, female mate choice can exert a considerable effect on male mating strategies. Asynchronous estrus and female mate choice allows females to avoid mating with natal males and to mate with more than one male to ensure fertilization during their short estrous period. Both of these factors may lead to increased reproductive success. Female avoidance of natal male's mating attempts may prompt natal male transfer. However, natal males can also remain in their natal troops but establish relationships and mate with females in adjacent troops. If there is a first mate advantage, this latter strategy may not lead to long-term reproductive success, since nontroop males appear to mate last. Eventual transfer from natal troops would be expected and necessary for males to attain the status of central male.

Female choice of nontroop males and intense intermale competition limits the chance of a single male to monopolize mating opportunities and to ejaculate more than once. The central male may attempt to circumvent this in a number of ways. He establishes close relationships with troop females throughout the year in order to monitor their reproductive state. He maintains the highest rank in the dominance hierarchy, allowing him to limit sexual monitoring by other males. He exhibits precopulatory guarding, thereby increasing his chance of being the first to mate when the female becomes behaviorally receptive. Finally, he may have longer postejaculatory guarding, resulting in the formation of a copulatory plug, which might impede fertilization by other mating partners. Subsequent males replace the former mating partner as quickly as possible, displace or remove previous copulatory plugs, and guard the female for as long as possible after their ejaculation.

Highly seasonal breeding species such as *L. catta* thus exhibit specialized mating strategies that include both direct and indirect male-male competition. However, further research on mating order and subsequent paternity, the effect of copulatory plug

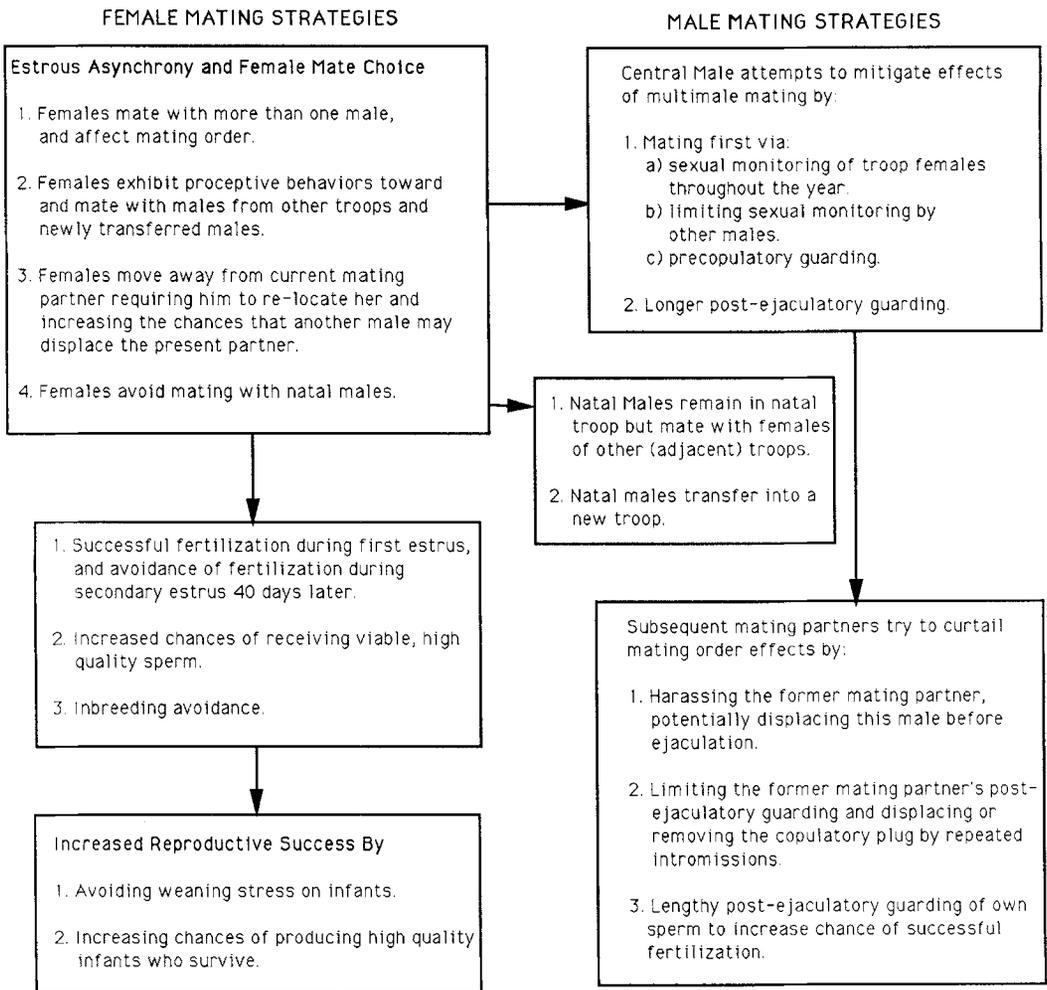


Fig. 3. Model of *Lemur catta* mating strategies.

formation in limiting fertilization by subsequent mating partners, sperm longevity, and especially the timing of ovulation relative to the onset of behavioral receptivity in females is needed to clarify these affects in seasonal breeders.

In conclusion, 1) females showed preferences in mating partners, favoring unrelated troop males or males from nearby troops and rejecting related individuals. 2) The mating order of male *L. catta* reflected the individual's social status and his relationship with troop females. Central males were able to mate first for a number of reasons, not all of them involving dominance. 3) Transfer be-

havior in ringtailed lemur males is a complex process involving several patterns. 4) Maternal expertise differed with experience, with multiparous females demonstrating more appropriate behaviors during and after parturition than primiparous females.

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