Male Life History and Intergroup Mobility Among Ringtailed Lemurs (*Lemur catta*)

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Lemur catta *shares a male-biased dispersal pattern with most primate species and the majority of mammals. Individuals in a free-ranging population of ring-tailed lemurs were captured, marked, released, and monitored for a 40-month period. Sixty-four percent of the males (43 of 67) migrated or were missing within this period and all nine censused groups were affected by migration. Males migrate from their natal group and then may migrate again after reaching full adult body weight. Full-sized adult males migrate at a rate of 0.28 per year or once every 3.5 years and may change groups a number of times during their life. Migrations occurred within a 6-month period, ending just after the mating season. However, there is no direct connection between mating success and male migration. Females mate with transferring males, with group males, and with visitors from adjacent groups. The age-related pattern of male migration and the occurrence of extragroup mating in* Lemur catta *is similar to that described for several species of macaques.*

INTRODUCTION

Although there has been a great deal of research on the demography and social organization of monkeys and apes, little is known about the demographics of Malagasy group-living Strepsirhini. These primates evolved in isolation from other members of the order for at least 60 million years. Among lemurs are the only prosimian primates which are diurnal and whose ecology and behavior often parallel those of many monkeys and

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apes. *Lemur catta* (the ringtailed lemur) occupies a niche very similar to that of baboons and macaques and also shares several characteristics of social behavior with these Old World monkeys (Sussman, 1977). For example, ringtailed lemurs live in relatively large, multimale, female-resident groups. However, in other ways, the ringtailed lemurs are unlike most monkeys. Females are agonistically dominant to males (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor and Sussman, 1986; Taylor, 1986; Sauther, 1991), animals mature relatively quickly (at 2-3 years of age) (Taylor, 1986, Sussman, 1991), and there is a very short breeding season each year (Jolly, 1966; Evans and Goy, 1968; van Horn and Resko, 1977; Koyama, 1988; Sauther, 1991).

In the majority of mammalian species, including most primates, males have the higher probability of leaving their natal group and of subsequent dispersal (Greenwood, 1980; Pusey and Packer, 1986; Shields, 1987). As first noted by Budnitz and Dainis (1975) and Jones (1983), *Lemur catta* shares this pattern of male-biased dispersal. In this paper, I report results from the first 40 months of an ongoing study on the demography and social organization of ringtailed lemurs at the Beza Mahafaly Reserve in southwestern Madagascar, concentrating on the patterns of male migration. Among them, male migrations usually occur during a 6-month period each year, between December and May. Proximate causes for this periodicity in male migration are unknown. This paper covers three such migration periods.

Just as Sprague (1992) found in Japanese macaques, preliminary data suggest that, although male migration among ringtailed lemurs generally coincides with the mating season, dispersal patterns may not confer short-term mating advantages. As in *Macaca fuscata*, ringtailed male transfer may reflect age-specific strategies related to maintaining a social position appropriate to the age of an individual.

Ringtailed lemur 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). The main body of a group consists of the adult females, their young, and one to three "central" adult males (Sauther, 1991). There also are a variable number of peripheral males that rank below the central males agonistically (Jolly, 1966; Sussman and Richard, 1975; Budnitz and Dainis, 1975). Central males spend more time in proximity and in social interaction with group females than peripheral males do. From our recent censuses (Sussman, 1991), it appears that peripheral males include recently transferred males, old males, and some young natal adults. There are separate agonistic dominance hierarchies among males and among females (Jolly, 1966; Taylor, 1986).

STUDY SITE AND POPULATION

The Beza Mahafaly Reserve was established in 1978 and decreed a Special Government Reserve in 1986 (Richard et al., 1987). Beza Mahafaly is the field site for a cooperative interuniversity project coordinated by the University of Madagascar, Washington University, and Yale University. The project was developed to promote conservation, education, research and development in southern Madagascar.

The reserve is divided into two parcels, one of 500 ha containing desert-like didierea forest (Parcel 2) and the other approximately 80 ha of gallery forest (Parcel 1). The study described here was conducted at the latter site. Because of its small size, we were able to enclose this parcel completely with a barbed wire fence and thus eliminate overgrazing by goats and cattle. Parcel 1 is dominated by trees of Tamarindus indica and is characterized by a relatively tall canopy forest bordering the Sakamena River. As one moves east to west from the river, the forest becomes more xerophytic, with trees that are smaller and more densely distributed.

Nine groups of ringtailed lemurs have been monitored over the past 40 months. this includes all groups within the fenced reserve and one group adjacent to it. Animals within and outside the reserve are not isolated from one another, and migration occurs freely between these and other groups. Over the 40 months 130 animals have been captured and marked for individual identification. At the time of the last census—July, 1990—only four adults in the nine groups (two females and two males, each from a separate group) had not been captured. Home ranges of groups average 32 ha, and the boundaries of home ranges overlap extensively with little or no area of exclusive use. Home range boundaries have not changed noticeably over the tenure of the study. A detailed description of methodology and of the field site is given by Sussman (1991). Methods used to calculate the demographic rates referred to in this paper are given by Caughley (1977) and the National Research Council (NRC) (1981).

Adult (and some subadult) animals are equipped with a nylon collar bearing a numbered plastic tag. The color of the collar identifies the group, the color of the tag identifies the sex of animals within each group, and the shape of the tag identifies the individual. In this way identification of an individual can be made quite easily and quickly, even when the tag number is not visible. Animals were darted by trained Malagasy guards using a Telinject blow gun (Sussman, 1991).

While the animals are tranquilized, the following information is collected: weight, reproductive state, general physical condition, internal body temperature, palmar dermatoglyphs, hair samples, external parasites, fecal samples, dental casts and a description of the dental condition, and body

measurements. The age of adult individuals is estimated by tooth wear. Immature animals are aged by their size. The population is divided into the following age classes: infant, 1 year old, 2 year old, young adult, young prime, prime adult, late prime, and old. The actual ages of animals in each of these classes cannot be determined until individuals of known age are recaptured. In captivity, ringtailed lemurs rarely live past 20 years (M. Jones, personal communication).

RESULTS

Ages of Migrating Males

In Table I are the results of censuses of the nine groups taken before the birth seasons in 1988, 1989, and 1990. The population of the reserve grew slightly during this period (growth rate = 1.13 individuals per year); the number of adults increased by five individuals over the 3-year period. The ratio of males to females is essentially one, and group size averages between 11 and 12 animals [group sizes average between 14 and 15 individuals after the birth season (Sussman, 1991)]. In Table I, I also summarize general patterns of male dispersal. Over the 3 years, all groups were affected by male migration.

The total number of adult males migrating or missing and the *maximum* migration rate (given in parentheses), which is the proportion of males which migrated or disappeared (NRC, 1981), in each of the 3 years is as follows: 20 in 1988 (0.47), 10 in 1989 (0.27), and 15 (0.33) in 1990 (Fig. 1). Infant mortality rates are similar in pattern to migration rates for these 3 years. Infant mortality for the first year after birth was 52% for infants born in 1987, 30% for those born in 1988, and 39% for infants born in 1989. High migration and infant mortality rates in 1988 correlate with a major drought in southern Madagascar in 1987–1988. the average yearly rainfall in the region is over 750 mm but was only 500 mm in 1987, the third lowest amount in the past 25 years.

The maximum migration rate for males over the 40 months of study was 0.36, or an average of once every 2.8 years. The patterns of male migration by age for all 3 years is given in Table II. Young adults (age 3–4 years) migrate at the highest rate—every 1.4 years. After an initial migration, males seem to settle for the next few years. Prime and late prime males migrated or were missing about once every 3.5 years. At the beginning of the study, in 1987, 43 adult males were captured and tagged. Seventeen (40%) of them were still in the original group in July 1990 (Table III). This includes none of the animals then classed as young adult (natal)

Table I. Census Data (Before Birth Season)

Group	1988 census					1989 census					1990 census				
	M	F	Total	A[a]	B[b]	M	F	Total	A	B	M	F	Total	A	B
Yellow	3	3	10	2		3	5	13			2+1[c]	7	14	2	
Yellow'	1+3	3	7			4	3	9			4	3	12		
Tan West	4	4	12	2		4	5	12	1		3	4	9	1	
Green	3+1	5	12	3	1	3+1	5	11	2	1	4+1	5	14	1	
Red	2+1	4	9	3		3+1	4	11	1		3+1	3	12	2	
Blue	3+1	2	9	2		3+1	3	9	2	1	2	2	7	2	
Black	2	4	8			3	4	8		±1[d]	3	4	11		
Tan East	3+1	4	11	2	1	3	4	10	1		4+2	3	13	2	2
Brown South	5+2	6	17		2	8	5	16	1		5+3	6	18		3
Totals	35	35	97	14	4	37	38	99	8	1	38	37	110	10	5
Mean	3.9	3.9	10.8			4.1	4.2	11.0			4.2	4.1	12.2		
Adult M/F ratio	1:00					0.98					1.02				

[a]The number of males emigrating from a group.
[b]The number of males entering a group from outside of the reserve population.
[c]A + in the column for males (M) indicates the total number of males attempting to immigrate into a group.
[d]One male transferred from Tan East to Black during the mating season, then returned.
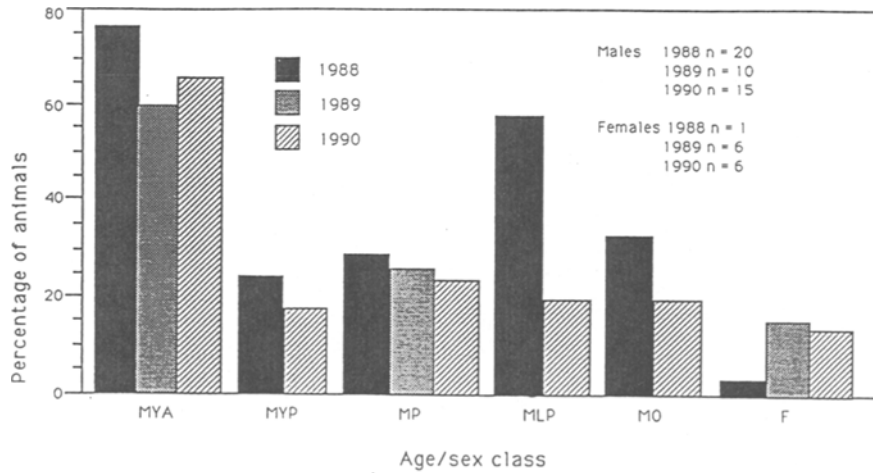
Fig. 1. Rates of migrating or missing animals, 1988, 1989, and 1990. MYA, young adult male; MYP, young prime male; MP, prime adult male; MLP, late prime male; MO, old male; F, female.

Table II. Totals, 1988–1990

	No. missing or migrating	No. in class	Max. migration rate	Avg. interval emigration (yr)
Young adult	16	23	0.70	1.44
Young prime	2	16	0.125	8.0
Prime	13	47	0.28	3.6
Old prime	5	17	0.29	3.4
Old	4	16	0.25	4.0
Age unknown	5	6		
Total	45	125	0.36	2.80
Females	13	112	0.12	8.62

Table III. Migration Among Originally Censused Males

	No. in same group	To neighboring group	Outcome unknown	Dead	Total No. in class	% in same group
Young adult	0	3	5	1	9	0
Young prime	4	—	—	—	4	100
Prime	7	3	5	—	15	47
Late prime	4	1	3	—	8	50
Old	2	—	4	—	6	33
Age unknown	—	—	1	—	1	—
Total	17	7	18	1	43	39

males, all of the young prime males, and 13 (43%) of the males in older age classes.

There was a total of 45 migration events by males during the study; this includes both animals that disappeared (fate unknown) and those that actually migrated (fate known) (Table IV). Forty-three adult males either attempted to migrate or were missing, and two of them took part in two migration events. The fates of 23 of them remain unknown and one young adult died after leaving his natal group. One young adult, natal male attempted to migrate in 1987 but returned to his original group at the end of the mating season. He did migrate in 1990. Fifty percent (10 of 20) of the males in prime age categories transferred between groups, and one of them changed groups twice.

The fate of a greater number of young adult and old males than of prime age classes remained unknown (Table IV). Only 4 of 16 (25%) of young adult males were successful in migrating, while the fate of 63% remains unknown. None of the old males were observed to transfer between known groups. These data suggest that males of different ages may have differing strategies, as well as different rates of success, in transferring between groups. It is possible that young adults are more vulnerable to predation (Sauther, 1989) and that old animals did not emigrate but instead died of natural or other causes.

Observations of Male Migration

Since the groups were monitored continuously between July 1987 and November 1988 and recensused only in 1989 and 1990, complete migration

Table IV. Fate of All Males Missing or Migrating Throughout the Study Period

	No.	Missing	Migrate	Attempt migrate, return	Attempt migrate, missing	Dead	% known to migrate
Young adult	16	9	4	1	1	1	0.25
Young prime	2	1	1				0.50
Prime	13	6	7				0.54
Late prime	5	2	2		1		0.40
Old	4	4					0.00
Age unknown	5	1	4				0.80
Total	45[a]	23	18	1	2	1	0.40

[a]The total number of migration events observed. Two individuals took part in two migration events.

events are known only for the earlier period. In a population of ringtailed lemurs at Berenty in Southern Madagascar, Jones (1983) observed most migrating males to move in pairs. At Beza Mahafaly, all transferring males that were observed either leaving a group and/or attempting to enter a new group did so with one or two other males. They coordinated their activities, leaving old groups and approaching new ones together. However, none of them which emigrated from the same group were still together when seasonal migrations had ceased. Solitary males were not seen.

In this study, I considered that an individual was successful at immigrating into a new group if he was still with them by the next birth season. This seems justified since most males attempted to migrate between December and the culmination of the brief mating season at the end of May. By the following birth season, in September–October, male migrations had ceased. By this time, males that had transferred were integrated into their new group, though normally as peripheral males.

To illustrate the complexity of male migrations, I give a brief description of observed movements of several males during the 1987–1988 migration period. Three pairs attempted to move into adjacent groups, but only one individual was successful in transferring on first attempt (Fig. 2). This

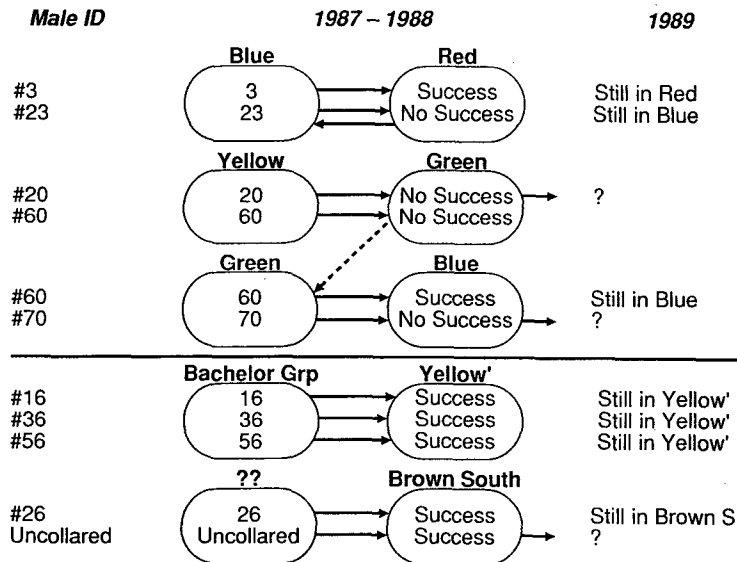| Male ID	1987 – 1988		1989
	Blue	**Red**	
#3	3	Success	Still in Red
#23	23	No Success	Still in Blue
	Yellow	**Green**	
#20	20	No Success	?
#60	60	No Success	
	Green	**Blue**	
#60	60	Success	Still in Blue
#70	70	No Success	?
	Bachelor Grp	**Yellow'**	
#16	16	Success	Still in Yellow'
#36	36	Success	Still in Yellow'
#56	56	Success	Still in Yellow'
	??	**Brown South**	
#26	26	Success	Still in Brown S.
Uncollared	Uncollared	Success	?

Fig. 2. Patterns of male migration, 1987–1988 season.

was a prime male (No. 3), which transferred from Blue to Red group. His partner, a natal male (No. 23), was unsuccessful and returned to his natal group (Blue). Both males of the second pair were unsuccessful in their initial attempt to transfer (from Yellow to Green). One of them (a natal male) subsequently disappeared, while the second (a late prime adult, No. 60) transferred successfully into a third group—blue. Another late prime male left his group (Green) and attempted, with No. 60, to transfer into Blue. He remained with this group for 3 months and then disappeared. Thus, none of these males, in which the whole process was observed, successfully transferred with a partner.

Two partnerships were successful in transfers, but the original group membership of these individuals is unknown. Two males joined a group (Brown South) from outside the study population, and the three males of an all-male group joined a recently split-off group—Yellow Prime. Whether this all-male group was composed of individuals which left the same group or joined together after being unsuccessful in transferring the previous year is unknown.

At Berenty, most males transferred into groups with fewer males (Jones, 1983). At Beza Mahafaly, there was a greater tendency for males to leave groups with high male-to-female ratios than with equal or lower ratios (Table V). Further, the number of males emigrating from the census population was greater than that joining it over the 3 years, and this was a major factor in equalizing the sex ratio (which was initially biased toward males). Males at Berenty transferred into adjacent groups (though 5 of 17 were unaccounted for) (Jones, 1983). The Berenty Reserve is quite isolated from any other forest area, and moving to distant groups would be extremely difficult. At Beza Mahafaly, most suspected transfer males were not seen in nearby groups and migrating, collared males have been spotted in forests 2 to 3 km from the reserve.

Male Dispersal During the Mating Season

Male migrations occur throughout the 6-month period between December and May, but there is heightened male dispersal during the brief breeding season, a 2- to 3-week period in May (Sauther, 1991). Besides mating with group males and transfer males or those attempting to transfer, females were observed to mate with temporary *visitors* from adjacent groups (males visiting the group to mate but returning to their own group most evenings) and with *mating season transfers* (males which joined neighboring groups during the mating season but returned to their own group at its end) (Table VI).

Table V. Adult Male-to-Female Sex Ratios and Total Number of
Males Entering or Leaving the Nine Groups During Three Mating
Seasons (N = 27 Groups)

Adult M/F sex ratio	Enter	Leave	Change in number of adult males	
2.50	1	2	−1	
2.00	0	2	−2	
1.80	0	1	−1	
1.66	0	2	−2	
1.66	1	2	−1	(net gain/loss in
1.66	1	2	−1	groups with more
1.50	0	2	−2	males = −11)
1.33	0	0	0	
1.33	0	0	0	
1.33	2	0	+2	
1.25	1	3	−2	
1.20	1	3	−2	
1.16	3	2	+1	
1.00	1	2	−1	
1.00	1	1	0	(net gain/loss in
1.00	1	1	0	groups with equal
1.00	1	2	−1	sex ratio = −2)
0.83	2	0	+2	
0.80	0	1	−1	
0.75	0	1	−1	
0.75	0	0	0	
0.75	0	0	0	(net gain/loss in
0.75	0	1	−1	groups with more
0.60	0	0	0	females = +1)
0.57	1	2	−1	
0.50	0	0	0	
0.33	3	0	+3	

In the two groups intensively studied by Sauther (1991), 35% of the observed matings were by nongroup males, involving three of the seven males observed copulating. The number of matings per male, among those males observed copulating, was not significantly different (Sauther, 1991, Table 3). However, in both groups, the central male was the first to copulate when a group female initially became receptive, followed by the second-ranked male. Transfer and/or nongroup males mated next. Sauther (1991) gives a detailed discussion of the possible relationships between this pattern of mating and reproductive success.

It is noteworthy in Table VI that two of the individual males discussed above, Nos. 60 and 23, were observed to mate in Green group in 1988. Male 60 was originally seen in Yellow. Although he mated in Green group in 1988, he was not successful in migrating into this group and moved on

Table VI. Observed Matings, 1988 (Adapted from
Sauther, 1991)

Male No.	Social status[a]	Female No.
	Green group	
10 Green	Alpha (central)	13, 33, 53
30 Green	Beta	13, 33
60 Yellow	Transfer	13, 33
23 Blue	Visitor	33
	Black group	
99 Black	Alpha (central)	02, 42, 82
19 Black	Beta	02, 42, 82
Tnt Blue	Mating transfer	02, 42, 82

[a]There is a linear dominance hierarchy among males.
See text for social status categories.

to Blue. In 1990, he transferred again, into Red (and is the only male thus far successfully transferring twice within the population). In 1988, male 23 attempted to move from his natal group Blue to Red. He was unsuccessful and returned to Blue. However, in that same year he was successful in mating in Green group and he subsequently transferred into Green in 1990.

Female Dispersal

There is evidence of a small amount of movement of females between groups. During 1987–1988, one female died and one was missing. In the following year, 4 of the 38 adult females were missing by the last census. Two of them disappeared from Black group and they were replaced by two unknown adult females. Unlike the transferring males, which remain peripheral and low-ranking upon entering a new group, the two 1989 immigrant females immediately assumed highest ranks in their new group. In 1990, 5 of 43 females were missing and 1 died; there were no new adult females in the population. This yields a maximum migrations rate of 0.12 for the 3 years combined. Assuming that none of the missing females died (an unlikely assumption), this would indicate that females transfer on the average at a rate of once every 8–9 years.

The actual rates of female migration are most likely much less than this, however. Of the 29 females originally darted in 1987, 22 (76%) are still in their original group. Seven of them (24%) are dead ($N = 2$) or missing ($N = 5$), and two of the missing individuals were very old when

first captured. No known females have transferred between groups. The average yearly mortality rate among adults at Berenty is about 0.08 (Mertl-Millhollen et al., 1979). If these seven females died over the past 3 years at Beza Mahafaly, the yearly mortality rate would be the same as that at Berenty and the migration rate would be about 0.04, or once every 22 years, longer than the normal life span of ringtailed lemurs.

One further change which affects female dispersion is group fission. At Beza Mahafaly, one group fission occurred in 1988. Group Yellow split, with three of the six adult females and one of the six adult males forming group Yellow Prime. Soon after this group fission occurred, three members of an all-male group transferred into group Yellow Prime and are still in that group. The two splinter groups still occupy the same home range but do not move together.

DISCUSSION

The ultimate causation of migration has been discussed by several authors, as have the potential proximate mechanisms (Greenwood, 1980; Pusey and Packer, 1986; Shields, 1987; Dunbar, 1988). In the ringtailed lemur, it could be assumed that sexual competition and mate choice are proximate driving forces for male transfer. Migrations begin well before and culminate just after the mating season. Resident males attempt to keep transferring males out of the group and female choice is a prerequisite to mating success (Jolly, 1966, 1984; Sussman and Richard, 1975; Taylor, 1986; Sauther, 1991). Female ringtailed lemurs either allow males to approach them sexually or actively present to a male. Any unacceptable male is rebuffed (Taylor 1986; Sauther 1991). In cases observed, resident central group males are allowed first access to receptive females. As found in a number of macaque species (Drickamer and Vessey, 1973; van Noordwijk and van Schaik, 1988; Paul, 1989; Sprague, 1992) and in baboons and vervets (Kummer, 1968; Hausfater, 1975; Packer, 1979; Henzi and Lucas, 1980; Smuts, 1985), there is a relationship between male dominance rank and age. In all six of the nine groups at Beza Mahafaly in which dominance relationships are known, the central, dominant male is in the Prime age category.

However, as in Japanese macaques (Sprague, 1992), there is no direct correlation between male transfer and mating success in any 1 year. Females mate with peripheral males, with recently transferring males (some of which do not remain with the group), and with males "visiting" from adjacent, neighboring groups (Sauther, 1991). In a recent study of polygynous red-winged blackbirds (Gibbs et al., 1990), genetically based measures

of reproductive success showed that individual males realized over 20% of their success from extragroup fertilizations and that this form of mating behavior confounded traditional measures of male success. At Beza Mahafaly, 35% of the observed matings in 1988 were by extragroup males.

In ringtailed lemurs, females reject advances of closely related males and possibly unrelated natal males (Taylor and Sussman, 1985; Sauther, 1991). Since central males appear to hold a favored position within groups (i.e., most affiliative interactions with females, mating priority), males may transfer into groups in which attaining this status seems more possible. However, there may be a variety of reasons that entering a new group may heighten the reproductive potential of a male at various stages in his life. Male transfer seems to be as much related to local and temporal demographics, to life history strategies, and to social role at various stages of a male's life as to immediately improved mating success during any 1 year.

The age at which a male migrates may depend upon a number of factors and may be related to demographic and environmental conditions. The general pattern of male migration found in *Lemur catta* is similar to that found in most cercopithecine species and many other primate species that live in multimale groups (Pusey and Packer, 1986), as well as many other mammals (Greenwood, 1980; Shields, 1987). Nonnatal males comprise most of the sexually mature males in a group, all males depart from the group in which they were born, and some males live in several groups during their lives.

The large number of males migrating in 1988 might be due to increased dispersal during the environmental stress caused by the drought conditions during the preceding year. However, differences in migration rates from year to year also might be related to short-term demographic stochastics (e.g., the ratio of emigrants:immigrants in the population or the number of males of certain age groups) or simply to chance variation from year to year (Altmann and Altmann, 1979; Dunbar, 1979; 1984; Rowell, 1979). It has been suggested that infanticide may be an important factor in ringtailed lemurs (Pereira and Izard, 1989; Pereira and Weiss, 1991), and the relationship between infant mortality and male migration might be interpreted by some to be responsible for this correlation.

However, it must be stressed, that after many long-term, intensive studies with identified individuals, infanticide has never been observed among ringtailed lemurs (Jolly, 1966; Sussman and Richard, 1974; Taylor, 1986; Gould, 1990; Sauther, 1991), and in the majority of long-term studies, male targeting of infants for aggression has *not* been observed in wild (Gould, personal communication; Sauther, personal communication; personal observations) or in captive groups (Taylor, personal communication; Lessnau, personal communication).

Natal ringtailed males leave their mother's group at between 3 and 5 years of age. It appears that after this, young prime males may not move for a few years. This pattern is also similar to that reported for *Macaca fascicularis* and *M. fuscata* (van Noordwijk and van Schaik, 1988; Sprague, 1992) and may, as in these macaques, be related to the achievement of adult weight and status. The average weight of young adult ringtailed males in this study is 1979 g (range = 1700–2300 g; n = 14), while that of older males is 2254 g (range = 1850–2775 g; n = 41), (P < 0.001, Student t test). Prime and late prime males migrate, on average, every 3.5 years and often leave even though they may occupy a central position in the group.

Both at Berenty (Jones, 1983) and at Beza Mahafaly, the normal pattern of male transfer is in pairs or triplets. Solitary males were not seen. Migrating in pairs or in groups is common in many species of primates (Cheney, 1983; Pusey and Packer, 1986). As in other species, migrating ringtailed males are vulnerable to predation and are the subject of attack by resident males. By transferring together, individuals, especially more vulnerable natal males, may improve their ability to spot predators and to defend themselves against attack by group males.

The average number of years (2.8) that an adult male stays in a group corresponds with the age of sexual maturity of female ringtailed lemurs (2.5 years). Furthermore, as stated above, female mate selection is the rule in this species. This provides general support for the hypothesis that increasing familiarity and consanguinity may lead to fewer potential sexual partners within the group and precipitate the preference for strange males and the ejection by females of older males from groups in which they have long been resident (Itani, 1972; Henzi and Lucas, 1980; Clutton-Brock, 1989; Huffman, 1991). However, the average of 2.8 years includes natal male migration and most adult males remain in groups longer than this average. For example, as stated above, 43% of the prime adult males first captured in this study are still in their original group. Thus, it is obvious that many males do not fit the typical pattern and that varying strategies are used by different animals in different contexts. Furthermore, as in some species of macaques (Mehlman, 1986; Moore, 1992; Sprague, 1992), many matings are performed by nongroup males. It will take longer studies, in which the life histories of many individuals are known, before we can understand alternative mating strategies used by ringtailed lemurs of both sexes.

With regard to the effects of dispersal on population structure, the type of "trickle migration" (Dunbar, 1988) observed in *Lemur catta* appears to be important in smoothing inequalities in sex ratios or in numbers of animals within groups, as well as minimizing inbreeding and randomizing gene flow. Group fission may be more important than male transfer in

adjusting population size over larger areas. If population growth occurs within one area, emigration of a splinter group, often to less desirable habitat, may be a means of maintaining suitable population densities (Dunbar, 1988). However, this might be a slow process in populations in which groups share a large part of their home range. At Beza Mahafaly, the two splinter groups, Yellow and Yellow Prime, still share home ranges. However, it appears that the two groups are expanding their ranges slightly to the west of the reserve and Yellow Prime usually is located to the west of group Yellow. We shall continue to examine the dynamics of this group fission.

SUMMARY

(1) Ringtailed lemurs live in female-resident groups with males regularly migrating between groups. Although some female dispersal occurs, it is rare.

(2) the overall rate of male migration may vary from year to year, possibly in relation to climatic and environmental conditions, with more migration and instability during years of lower resource abundance.

(3) Young adult males migrate from their natal groups, usually in their third or fourth year. In some rare exceptions, they may remain in the natal group until 5 years of age.

(4) After this initial migration, young prime males (probably 5-7 year olds) remain in their new group over the next few years, and this may correspond with the attainment of full mature body weight and full adult status.

(5) Upon reaching prime age class, males migrate, on average, every 3 to 4 years. (Females first give birth at the age of 3 years). To data, no prime or older male has been known to stay in the same group for longer than 5 years, though 43% of the adult males tagged in 1987 were still in their original groups in 1990. There is little difference in the rates of migration between prime and late prime males but prime males may be the most successful age class in transferring into new groups and hold central positions in all groups in which this status is known ($n = 6$).

(6) Although old males migrated or were missing about as much as prime males, none are known to have successfully migrated between groups or immigrated into the population. It appears that upon reaching old age, males may transfer infrequently.

(7) There may be a general tendency for male migrations to equalize the sex ratios in groups and in the general population. Males transfer, normally in pairs or trios, into both neighboring and distant groups.

(8)Females mate with group males, transferring males, males transferring just during the mating season, and temporary visitors (Sauther, 1991). Previous studies have shown that female choice is a prerequisite to mating success.

(9) The proximate function of male dispersal in Lemur catta superficially appears to be sexual mate choice and male competition. However, male migration may be related to age-related strategies for successful integration into a group at various life stages and correspond to increasing social skills and maturation. The long-term adaptive significance may involve equalizing sex ratios within groups and populations, avoiding inbreeding, and ensuring a high level of genetic variability by maximizing random gene flow.

(10) Generally, male life histories, patterns of male migration, and extragroup mating in Lemur catta are similar to those described for some species of macaques, baboons, and vervets, as well as many other species of mammals. Upon reaching sexual maturity, young males leave their natal group and join other groups at low rank. Young males then settle into a new group where they spend several more years maturing. Upon achieving full mature body weight and status, prime males may either migrate or stay in their group depending upon a number of factors, some of which are likely to relate to the potential of becoming a central male and to mating possibilities. Old males are not able to maintain a central position in the group and settle for subordinate or peripheral status. There is a relationship among male migration, age, size, mating success, and position in the male hierarchy, but this relationship is not a simple one. Long-term studies of the entire life cycle of identified individuals are needed in order to understand various age-related strategies for successful group living and for mating success.

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