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Demography and Social Organization of Free-Ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar

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ABSTRACT In 1987, a long-term study of the demography of *Lemur catta* was begun in southern Madagascar. Eighty-five ringtailed lemurs were captured, marked, and released. Adult age classes were estimated using patterns of dental attrition. Including young, 155 individuals from nine groups were identified and monitored over 18 months. The study population of the reserve remained stable, with a growth rate of 0.98. Group sizes ranged from nine to 22 individuals (mean 14). Home ranges were larger (32 ha) and population densities lower (135/km^2) than those for previously studied populations, and there was a relationship between habitat quality (e.g., no. of large trees) and these factors. At the beginning of the study, there were more adult males than females, but the sex ratio reached 1.00 by the last census. Females first gave birth at 3 years of age, and 80% or more of the females gave birth in 2 consecutive years. Fifty-two percent of the infants died in the first year and, given preliminary findings, only 40% of those born reach adulthood. Age-specific fertility patterns were similar to those reported for anthropoid primates. Forty-seven percent of the adult males migrated or were missing within a year. This included 78% of the 3–4 year olds and 38% of older age classes. No females were observed to migrate. One group split during the study. Demographic patterns are discussed and related to patterns in other populations of ringtailed lemurs as well as in anthropoids.

Although a number of demographic studies have been conducted on free-ranging anthropoid primates (see Richard, 1985, and Dunbar, 1986, 1988, for recent reviews), there are few demographic data available on natural populations of prosimians. Thus, we know little about the dynamics of these populations or life-history variables in these species. Furthermore, studies of primate populations in which individuals are tagged for long-term identification are still extremely rare. Knowledge of life-history tactics and population dynamics is critical to an understanding of the relationships that exist between animals and their environment (Caughley, 1977; Stearns, 1977), as has been demonstrated in a number of primate studies (e.g., Otis et al., 1981; Strum and Western, 1982; Ohsawa and Dunbar, 1984; Dunbar, 1987; Cheney et al., 1988). Demographic patterns also play a key role in the social behavior and organization of primate populations (see, e.g., Packer, 1979; Dunbar, 1984, 1985; Altmann et al., 1988). As natural plant communities continue to decrease, these data will become increasingly important in our attempt to conserve remnant primate populations.

In this paper, I report preliminary results of a proposed long-term study of the demography of a population of free-ranging *Lemur catta* in the Beza Mahafaly Reserve in southern Madagascar. Apart from a parallel study being conducted on *Propithecus varreauxi* in the reserve (Richard and Rakotomanga, in press), no other demographic study of individuals tagged for long-term identification exists for natural populations of prosimians.

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L. catta is one of the most studied of the Malagasy lemurs and a population, living in 97 ha of the Berenty Reserve in southern Madagascar, has been censused intermittently since 1972 (Budnitz and Dainis, 1975; Mertl-Millhollen et al., 1979; Jolly et al., 1982; O'Connor, 1987). However, individuals in this population have not been marked or consistently identified, and there have been lapses of several years between censuses. Thus many basic questions have remained unanswered. For example, we need to know more about fertility rates, age of females at first birth, interbirth intervals, and infant mortality rates. We know little about general mortality rates and rates of population growth. We know that individuals migrate between groups, but we do not know rates or patterns of migration. Do all males migrate, what are the ages of migrating individuals, do natal males migrate, do animals disperse to neighboring or distant groups, and do females migrate? These are some of the questions we are addressing in this study. Until we have answers to these basic questions, such things as relationships between population dynamics and environment, or life-time reproductive strategies of individuals, will remain unknown.

STUDY SITE

Research was conducted in southwestern Madagascar at the Beza Mahafaly Reserve. This 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 School of Agronomy of the University of Madagascar, Washington University, and Yale University. The project was developed to promote conservation, education, research, and development in southern Madagascar.

Beza Mahafaly is located ca 23°30′S lat., 44°40′E long., about 35 km northeast of Betioky-Sud (Fig. 1). The reserve is divided into two parcels, one of 500 ha containing desert-like didierea forest and the other approximately 80 ha of gallery forest. The reserve boundaries are fairly arbitrary and are contiguous with forests of the same type throughout the region. The study was conducted at the latter site, referred to as parcel 1. This parcel is completely enclosed by a barbed-wire fence. It is dominated by *Tamarindus indica* trees 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 in character, with trees becoming smaller and more densely distributed (Sussman and Rakotozafy, in preparation). Major tree species include *Azima tetracantha, Crateva excelsa, Acacia rovumae, Euphorbia tirucalli, Quivisianthe papinae, Salvadora augustifolia,* and a number of species of *Grewia*. Tree species endemism is about 70%. One square hectare paths have been cut throughout this portion of the reserve, and paths are color coded and trees are marked to facilitate locating groups and mapping day and home ranges.

Southern Madagascar is characterized by a dry season and a wet season, although the amount of rainfall can vary tremendously from year to year. Annual rainfall in the region of the reserve is about 750 mm, of which 600 mm falls during the austral summer, November–March. The wet season is also characterized by high ambient temperatures, averaging between 34°C and 35°C, and reaching highs of 48°C. Average temperatures during the driest and coolest months (June–August) range between 23°C and 30°C and can fall to 3°C at night. During this time, conditions are very dry, and most tree species lose their leaves. Annual temperatures average 25°C. These data are from the meterological station at Betioky-Sud (1951–1980) and do not reflect microclimatic differences that might occur between this station and the reserve.

METHODS

Between June, 1987, and February, 1988, nine groups of *L. catta* were censused and monitored. This included all groups that ranged mainly within the 80 ha fenced portion of the reserve and one group adjacent to it. Animals were darted using a Telinject blow gun and tranquilized with 2 cc of ketamine hydrochloride. These are high doses, comparable to those given to 25 kg baboons (Phillips-Conroy, personal communication), but smaller amounts proved to be insufficient. A total of 80 animals were captured and, including five animals caught in a previous study (Ratsirarsan, 1987), 85 animals are now marked for individual identification. Juveniles were relatively easy to identify and were not routinely darted. Only three adults in the nine groups were not captured. Groups were recensused by M. Sauther and J. Kaufmann in November, 1988. Including infants and juveniles, a total of 155 individuals were identified during

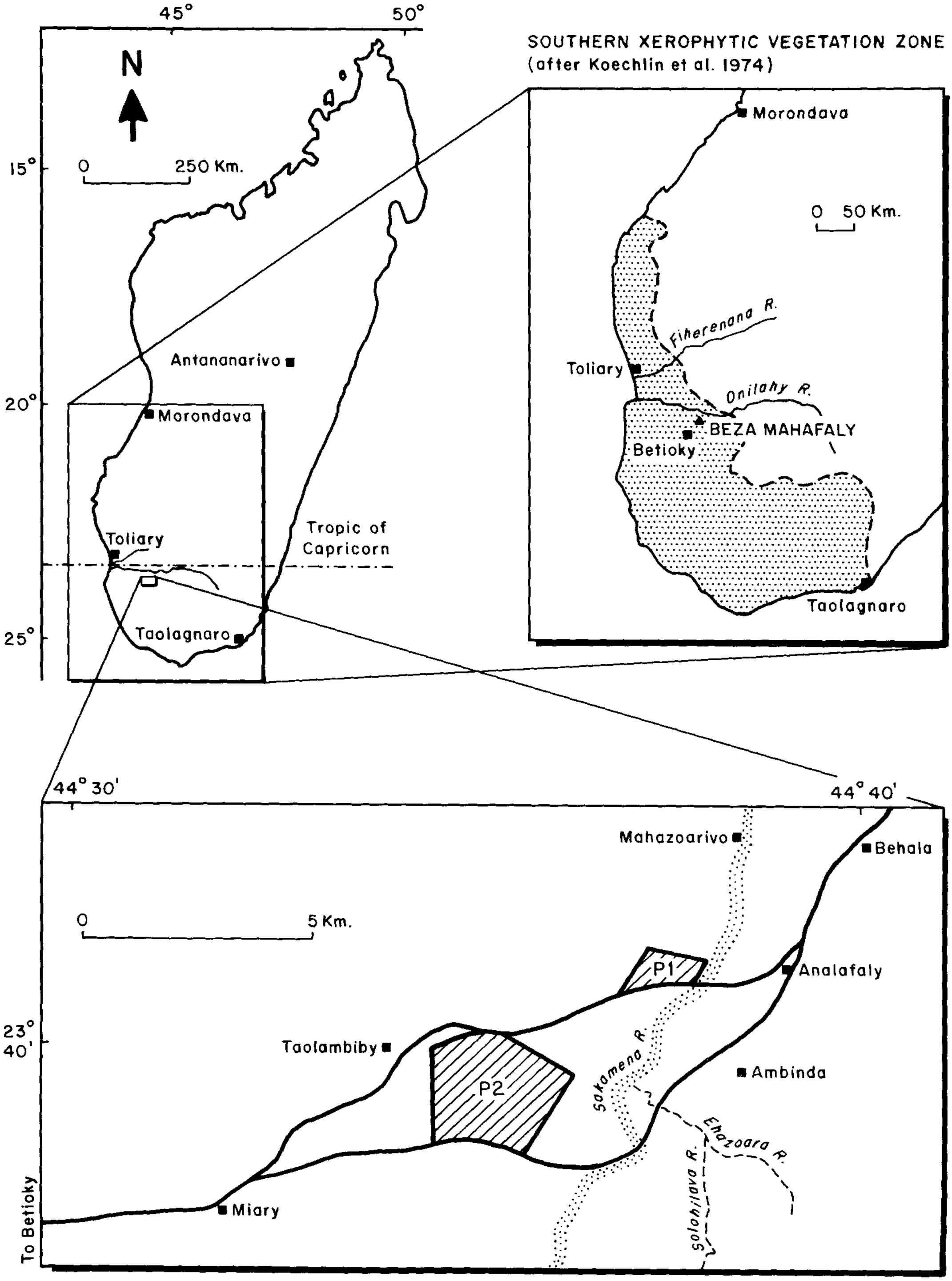


Fig. 1. Map of the location of the Beza Mahafaly Special Reserve.

this study, including all members of nine groups.

Each animal was given a nylon collar with a numbered plastic tag. The color of the collar identified the group, the color of the tag identified the sex of animals within each group, and the shape of the tag identified the individual. In this way the identification of the individual could be made quite easily and quickly, even when the tag number was not visible.

While the animals were tranquilized, the following information was collected: weight, reproductive state, general physical condition, internal body temperature, dermatologlyphs, hair samples, external parasites, fecal samples, dental casts and a description of the dental condition, and body measurements. Ear notches were given to many individuals, but natural marks made these difficult to use for identification. The age of adult individuals was estimated by tooth wear. Immature animals were aged by their size. The population was divided into the following age classes: infant, 1 year old, 2 year old, young adult (3–4 years old), young prime, prime adult, late prime, and old. Most *L. catta* are born within a 5 week period each year, and age cohorts in the immature age classes are quite distinct. Determinations of relative age classes were usually made independently by two or more observers, and rarely did observers disagree. However, estimates such as these can be subject to error, and the number of years represented by each adult age class is impossible to determine at this point.

RESULTS

Demographic structure

Tables 1–3 present the composition of censused groups at three different times over an 18 month period: just after the birth season in September, 1987; in January, 1988, during male migrations; and after the 1988 birth season in November. Eight heterosexual groups and one all-male group were included in the first census (Table 1). By January, 1988, three females and one male had split from Yellow group, forming group Yellow Prime (Table 2). This also was during the period (December–May) when some males were attempting to change groups. By this census, 11 males emigrated or were missing from the population, and four new males had migrated into it. Other males changed groups within the study population, including the three males from the all-male group (Brown B) who joined splinter group Yellow Prime. Five (20%) of the 1987 infants had died by this second census (Table 2). By November, 1988, dispersing males had settled into new groups (although not necessarily the group they had originally attempted to enter), and the 1988 crop of infants was born. Thus differences between censuses reflect births, deaths, age changes, male migration, and group fission. The dynamics of these changes will be discussed in the following sections.

Table 4 summarizes key statistics reflecting the social structure of this population during the three census periods and compares them with data from previous studies.

TABLE 1. 1987 census (after the birth season)[1]

Group	M	F	I	JM	JF	J?	Total
Yellow	6	6	3			3	18
Brown B	3						3
Tan West	5	4	3	3	1		16
Green	5	3	3	3	3		17
Red	4	3	3	3	1		14
Blue	5	2	2	1	1		11
Black	2	3	3	1	1		10
Tan East	5	4	4	1	2	2	18
Brown South	4	4	4	3	2		17
Totals	39	29	25	15	11	5	124
Mean	4.5	3.6	3.1		3.9		15.13
M/F ratio = 1.34							

[1] In this and the following tables M, male; F, female; I, infant; JM, juvenile male; JF, juvenile female; and J?, juvenile of unknown sex.

TABLE 2. 1988 census (during male migrations)

Group	M	F	I	JM	JF	J?	Total	1	2
Yellow	3	3	2			2	10	−2	
Yellow Prime	1 + 3	3	1			1	9		
Tan West	3	4	3	2	1		13	−2	
Green	3 + 2	3	2	3	3		16	−2	+1
Red	2 + 2	3	3	1	1		7	−3	
Blue	2	2	1	1	1		7	−3	
Black	2	3	2	1	1		9		
Tan East	5 + 1	4	3	1	2	2	18		+1
Brown South	4 + 2	4	3	3	2		18		+2
Totals	35	29	20	12	11	5	112	(−11)	(+4)
Mean	3.9	3.2	2.2		3.1		12.4		
M/F ratio = 1.21									

[1] This column includes the number of males emigrating out of a group.

[2] Indicates the number of males entering a group from outside of the reserve population. The + in the column for (M) indicates the total number of males attempting to immigrate into a group; thus for Green group, two males left the group and two males entered the group, one from outside of the reserve.

TABLE 3. 1988 census (after the birth season)[1]

Group	M	F	I	JM	JF	J?	Total
Yellow	3	3	3		2	2	13
Yellow Prime	4	3	2				9
Tan West	4	4	1	2	2		13
Green	4	5	5	2	1		17
Red	3	4	3	2			12
Blue	4	2	1	2	1		10
Black	2	4	4	2			12
Tan East	4	4[1]	4[1]	1	2		15[1]
Brown South	7	6	5	2	2		22
Totals	35	35	28	13	10	2	123
Mean	3.9	3.9	3.1		2.8		13.7
M/F ratio = 1.00							

[1] A Tan East female and her infant died shortly after the 1988 birth season, leaving 13 animals in this group at the end of the study

TABLE 4. Group structure of censused Lemur catta *populations*

	Beza Nov. 87	Beza Feb. 88	Beza Nov. 88	Previous studies[1]
No. of groups	8	9	9	
Avg. group size	15.1	12.4	13.7	13.4 (n = 57)
Mean No. adult M	4.5	3.9	3.9	5.2 (n = 10)
Mean No. adult F	3.6	3.2	3.9	6.0 (n = 10)
Mean No. infants	3.1	2.2	3.1	2.9 (n = 10)
Mean No. juveniles	3.9	3.1	2.8	3.3 (n = 10)
Adult M/F ratio	1.34	1.21	1.00	0.87 (n = 10)
Range M/F group	0.67-2.5	0.67-1.67	0.5-2.0	0.5-1.5 (n = 10)
Immature/all adults	0.82	0.75	0.76	0.55 (n = 10)
Immature/adult F	1.93	1.65	1.51	1.03 (n = 10)
Total population	124	112	123	
Total Beza Mahafaly population just before 1988 birth season = 95				

[1] Jolly (1966, 1972); Sussman (1974); Budnitz and Dainis (1975); Mertl-Milhollen et al. (1979); Jolly et al. (1982).

Average group size was about 14 animals in the nine groups and individual groups ranged from nine to 22 animals. This is similar to results from previous censuses in which groups have averaged about 13 and ranged from five to 27 individuals. Adult sex ratios of ringtail groups normally are close to 1.00. The Beza Mahafaly population, although it began with more males than females, reached an equal ratio by the last census as the result of female maturations and adult male migration (see below). The total population size after the two birth seasons remained essentially stable, 124 animals in November, 1987, and 123 in November, 1988 (growth rate = 0.98). However, because of infant mortality and male emigration, the population dropped to 112 animals by January, 1988, and reached a low of 95 animals just before the 1988 infants were born.

Six of the nine groups had home ranges located almost entirely within the fenced portion of the reserve. During the first 8 months of the study, the home ranges of groups bordering the Sakamena River averaged 17 ha, whereas those found mainly in the dryer section of the forest averaged about 32 ha (Fig. 2). Over the total 18 months, two of the river groups enlarged the size of their ranges (to 31 and 26 ha, respectively) especially to feed on the fruit of *Salvadora augustifolia* trees during October and November, which are located only in the dryer portion of Parcel 1 (Fig. 3). A third river group (Red) extended its range to the south of the fenced portion of the reserve. Including this seasonal expansion, the average home range of five groups (whose ranges were known over 18 months) was 32 ha (range 26–35 ha). These ranges are much larger than those previously reported for *L. catta* living in undisturbed habitats (6–23 ha). As was found in the Berenty population, the home ranges of groups at Beza Mahafaly had highly overlapping boundaries. In the study

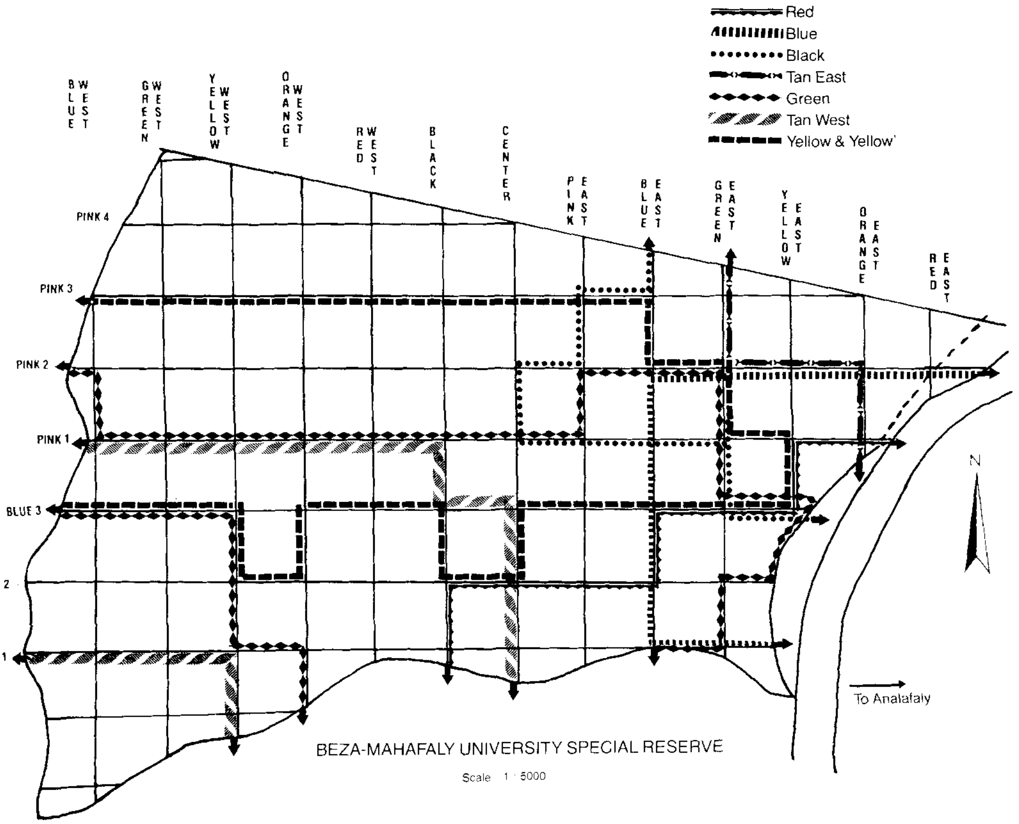


Fig. 2. Map of the home ranges of groups within the reserve.

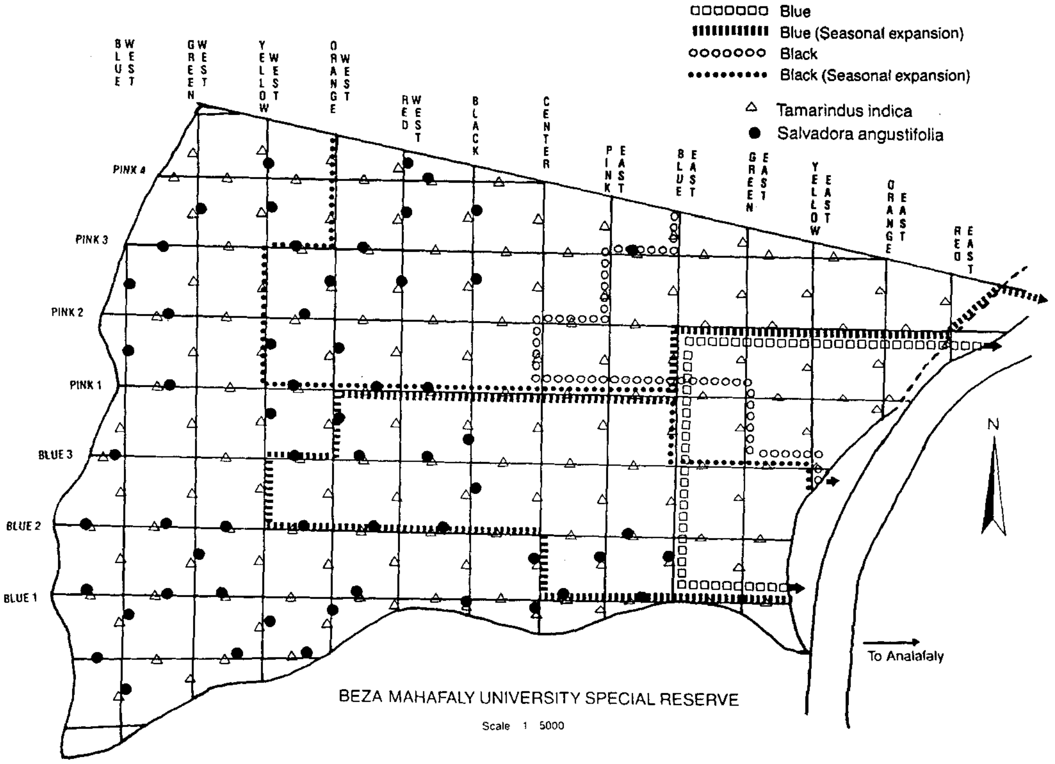


Fig. 3. Map of primary and seasonally expanded home ranges of groups Black and Blue, and the distribution of large *Tamarindus indica* and *Salvadora augustifolia* trees along grid paths.

TABLE 5. Home range size and densities

	Beza Mahafaly	Previous studies[1]	Disturbed forest O'Conner (1987)
Avg. home range size (ha)	25 (n = 6) 32 w/seasonal expansion (n = 5)	10.34 (n = 5)	23.4 (n = 2)
Range (ha)	16-35	5.7-23.1	12.2-34.6
Population density (per km^2)	90-135	147-350	17.4
Biomass[2] (kg/km^2)	200	—	48.7

[1] Jolly (1966), Sussman (1974), Budnitz and Dainis (1975).

[2] Biomass at Beza Mahafaly is based on average adult weight of 2,211 g (n = 65): male avg. = 2,213 g (n = 41), female avg. = 2,207 g (n = 24), J2 avg. = 1,673 g (n = 12), J1 avg. = 1,175 g (n = 2). Biomass reported by O'Conner was based on captive adult weights from Tattersall (1982) (avg. = 2,760, n = 11).

population, groups had few or no areas of exclusive use.

Table 5 summarizes data on home range sizes, population density, and biomass. The population density was estimated to be approximately 125–135/km^2 just after the birth seasons (using the eight groups with home ranges within the 80 ha fenced reserve). Four months after the birth season, density was about 115/km^2 and just before the birth season about 90/km^2. These densities are much lower than those reported for other ringtailed lemur populations in undisturbed areas (147–350/km^2). However, O'Connor (1987) found an extremely low density (17/km^2) in a disturbed and previously hunted forest. The biomass of ringtailed lemurs at Beza Mahafaly was approximately 200 kg/km^2.

The density of animals and of groups was higher in the portion of the forest containing lush gallery forest bordering the Sakamena River (Fig. 2), reaching about 175/km^2. This gallery forest differed in tree species composition and in density from the transitional vegetation to the west of the river, containing half as many individual trees but 2.5 times as many large canopy trees over 25 cm diameter at breast height (dbh) (230 vs. 90/ha) (Sussman and Rakotozafy, in preparation). A relationship between habitat quality and home range size was also reported for *L. catta* at Berenty. One group living in the lush gallery portion of this forest had a home range of 8.1 ha, and a second group of similar size living in a dryer portion of the forest had a home range of 23.1 ha (Budnitz and Dainis, 1975; Budnitz, 1978), and the density of ringtails is over three times higher for groups near the river (O'Connor, 1987).

The sizes of groups in the two microhabitats at Beza Mahafaly did not differ significantly, whereas home range sizes in the two habitats were significantly different ($P < .001$, Student's t test). Given the distribution of trees at Beza Mahafaly, all else being equal, groups living in the dry portion of the forest would need home ranges of approximately 37 ha to have the same number of large trees (about 3,450) as groups living near the river with home ranges of 15 ha. This does not differ greatly from the actual home range sizes of the groups in question.

Since the boundaries of all the groups do not fall completely in one microhabitat or another, a better comparison of habitat quality might be made by estimating the number of trees in each hectare within the range of a given group. Two of the groups (Black and Green) were studied intensively for 13 months (Sauther, in press) and their ranges were the best known. Black had a home range of 20 ha (excluding seasonal expansion), containing an estimated 4,460 large trees, and Green had a range of 34 ha, with an estimated 4,600 large trees.

Birth rate and infant mortality

L. catta females are sexually receptive for 1–2 days (Van Horn and Resko, 1977), and most females normally mate within a 2–3 week period each year. In captivity, a female not impregnated during the first estrus, may cycle for up to 3 months (Evans and Goy, 1968). Births generally are restricted to a 2–3 week period. During the study, in both birth seasons, most infants were born between September 18 and October 25, with one or two females giving birth approximately 3–4 weeks later each year. There were no twins in either season, although twins are common at Berenty and in captivity (e.g., at the Duke Primate Facility, 27% of 148 births have been twins or, in one case, triplets; A. Katz, personal communication).

In 1987, 25 of the 29 adult females at Beza Mahafaly bore infants, and, in 1988, 28 of the 35 females did so, yielding birth rates of 0.86 and 0.80, respectively. Thus, as was reported previously (Budnitz and Dainis, 1975; Mertl-Millhollen et al., 1979), ringtails have a very high birth rate, and the majority of females give birth every year. Females at Beza Mahafaly did not give birth until their third year, although females in captivity commonly give birth at 2 years of age (Taylor, 1986; Katz, personal communication).

Age-specific fertility rates are given in Table 6. As can be seen for 1987 and 1988 combined, birth rates for prime adult females are very close to 1.00. Young adult females (3–4 years of age) have a slightly lower fertility rate than prime females over the 2 year period. Those females classified as old showed considerably lower fertility than other classes, with none of the four females in this category giving birth in 1988. In fact, two of these old individuals were the only females not giving birth in either year.

Although annual birth rates are very high, infant mortality is also relatively high (Table 7). Between the birth seasons of 1987 and 1988, 52% (13 of 25) of the infants died. Five (20%) of these had disappeared within the first month. Five of the 28 (18%) infants born in 1988 also were missing within 1 month. In this small sample, young prime and prime females had above average rates of infant survival and none of the infants born to old females survived the first year. High infant mortality also has been reported at Berenty.

Mortality

As always, causes of mortality are difficult to pinpoint. Probable causes of death among *L. catta* are seasonal malnutrition, parasite infestations, disease, accidents, and predation (especially by large birds of prey, domestic dogs, and, in some regions, humans). Table 8 gives the number of individuals in each age-sex class for the total population

TABLE 6. Age specific fertility rates

	1987			1988			
	No. adult females	Births	Fertility rate	No. adult females	Births	Fertility rate	1987 + 1988 fertility rate
3-4 years	4	4	1.00	8	6	0.75	0.83
Young prime	3	3	1.00	4	3	0.75	0.86
Prime	13	12	0.92	15	15	1.00	0.96
Late prime	3	3	1.00	3	3	1.00	1.00
Old	4	2	0.50	4	0	0.00	0.25
??	2	1	0.50	1	1	1.00	0.67
Totals	29	25	0.86	35	28	0.80	0.83

TABLE 7. Annual infant survival and mortality rates per age class of mother (1987-1988)

	No. of females	Births	Survivors	Survival rate	Mortality rate
3-4 years	4	4	2	0.50	0.50
Young prime	3	3	2	0.67	0.33
Prime	13	12	7	0.58	0.42
Late prime	3	3	1	0.33	0.67
Old	4	2	0	0.00	1.00
??	2	1	0	0.00	1.00
Totals	29	25	12	0.48	0.52

TABLE 8. 1987-1988 age classes

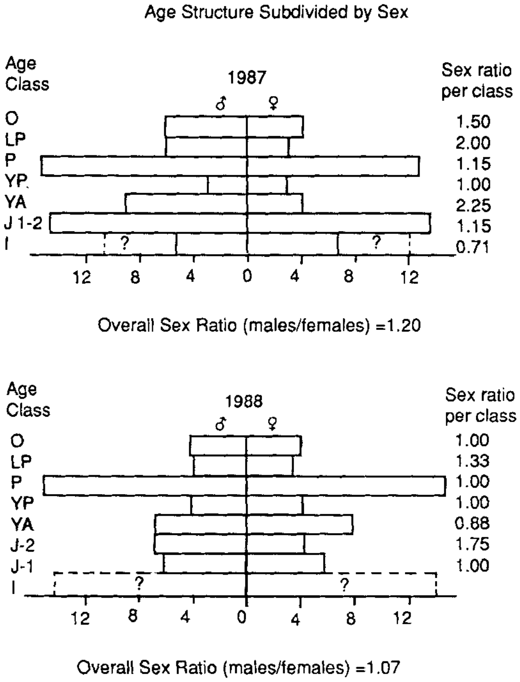
	1987 age classes				1988 age classes			
	F	M	?	1987 total	F	M	?	1988 total
Infants	7	5	13	25			28	28
Juvenile (1-2 years old)	13	15	3	31	10	13	2	25
Young adult	4	9		13	8	7		15
Young prime	3	3		6	4	4		8
Prime	13	15		28	15	15		30
Late prime	3	6		9	3	4		7
Old	4	6		10	4	4		8
??	2			2	1	1		2
Total	49	59	16	124	45	48	30	123

after the birth season in 1987 and 1988. Figure 4 represents an age profile by sex of the population during the same two periods. Except for the first 3 years, age-specific mortality rates and survivorship schedules cannot be determined from these data at present because the actual number of years per age class is unknown. However, these data will become available as the younger cohorts grow up and are recaptured over the years. The longevity record in captivity for ringtails is about 23 years, but adults rarely live past 20 years in captivity (M. Jones personal communication).

In comparing data presented in Table 8 and in Figure 4, there may be a differential mortality rate between males and females at 2–3 years of age, with death more common among females of this age class. If this is so, sex ratios even out in the adult age classes, and perhaps mortality is slightly higher among young adult males. However, any conclusions at this point about adult mortality patterns must remain highly speculative because of the possibility of year to year variations in mortality due to fluctuations in environmental conditions and because of the high rate of male migration. Sex ratios at birth are almost equal, as is the case in captivity (for example, there have been 57 females and 63 males born at the Duke University Primate Center over the past several years; Katz personal communication). However, sex ratios at birth also may vary greatly from year to year, and imbalances may be rectified by male dispersal.

A life table for three age classes is shown in Table 9. In this table emigrants are treated the same as deaths, so survivorship is most likely underestimated for the adult age class. Given these preliminary data, approximately 40% of the infants born would reach adulthood.

Between November, 1987, and November, 1988, one adult male and one adult female were found dead. A second female was missing and presumed dead, since female migration has not been observed. This gives a mortality rate of 0.07 for females and a minimum rate of 0.03 for males. However, 11 males were missing, and one was found dead after the first year, and the maximum adult male mortality might be 0.31. Since male migration is the norm in ringtails, it seems more accurate to assume that adult male and female mortality are somewhat similar, about 7–8% per year, and that a total of three or four adult males may have died. Mertl-Millhollen et al. (1979) report adult mortality of 0.08 at Berenty. If this assumption is true, the remaining eight or nine males emigrated from the study population.



Overall Sex Ratio (males/females) =1.20

Overall Sex Ratio (males/females) =1.07

Fig. 4. Age structure divided by sex of the population of *L. catta* in Beza Mahafaly in 1987 and 1988.

TABLE 9. Life table for three age classes (1987-1988)

	No. entering age class	No. dying or emigrating	Proportion leaving age class	Proportion surviving from birth to age
Infant	25	13	0.52	0.48
Juvenile	31	7	0.23	0.37
Adult	68	14	0.21	0.29

TABLE 10. Rates of migrating or missing males and females

	No. missing or migrating	Total no. in class	Maximum migration rate	Maximum migration per year
Young adult	7	9	0.78	1.28
Young prime	1	4	0.25	4.00
Prime	5	16	0.31	3.20
Late prime	4	7	0.57	1.75
Old	2	6	0.33	3.00
??	1	1		
Totals	20	43	0.47	2.15
Females	1	29	0.03	29.00

Migration and group fission

A total of 20 of the known adult males either attempted to migrate or were missing by the November, 1988, census (Table 10). As was stated above, the fate of 11 of these animals remains unknown, and one died. One young adult male attempted to migrate but was unsuccessful and returned to his original group. Seven males successfully migrated into new groups (four of these immigrated into the reserve population). Thus 47% (20 of 42) of the adult males attempted to migrate or were missing after the first year. The maximum number of successful migrations was 42% (11 + 7), and the minimum rate of migration was 16%. If the adult male mortality rate was 0.08 as predicted above, the rate of migration would be about 40%, with males migrating on average every 2.5 years. Jones (1983) reported a maximum migration rate of 30% for males in the Berenty population in one year. In the Beza Mahafaly population, one prime adult male first captured on September 19, 1985, (Ratsirarson, 1987) was still in the same group in November, 1988, 3.3 years later.

Only one of the adult females was missing in the last census. A second female died after the birth season in November, 1988. I assume that the former female also died. If she did migrate, the migration rate would be 0.03, and the rate of female migration would be once every 29 years.

Seventy-eight percent of the young adult males (3–4 years old) in the population migrated or were missing, compared with 38% of the adult males of older age classes. Young adults and late prime adults migrated (or were missing) more than average. Prime and young prime males were the least likely to migrate but also had the most known successes in migrating into new groups (Table 11). Thus, as in many primate species, young males leave their natal group and older adult males continue to migrate throughout their lives.

The common pattern of male migrations observed by Jones at Berenty was a pair of males migrating into an adjacent group. At Beza Mahafaly, ten transfers were followed, and no simple pattern emerged. All males initially left their group or entered a new group with one or two partners. However, partners did not always remain together. Three pairs attempted to move into adjacent groups, but only one individual among them was successful in transferring on first attempt (i.e., was still in the new group by the next birth season). This was a prime male who transferred from Blue to Red. His partner, a natal male, was unsuccessful and returned to his natal group (Blue). Both males of the second pair were unsuccessful in their initial attempt to transfer (into Green). One of these males (a natal male) subsequently disappeared, whereas 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 subsequently disappeared. Thus none of these males successfully transferred with a partner.

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

One further change occurred within the population during the tenure of the study. Group Yellow split, with three of the six

TABLE 11. Fate of males missing or migrating

	No. in class	Fate unknown	Successful transfer	Not successful (return)	Not successful (unknown)	Dead	Rate of known success
Young adult	7	2	2	1	1	1	0.29
Young prime	1		1				1.00
Prime	5	3	2				0.40
Late prime	4	2	1		1		0.25
Old	2	2					0.00
??	1		1				1.00
Totals	20	9	7	1	2	1	0.35

adult females and one of the six adult males forming group Yellow Prime. As stated above, soon after this group fission occurred, the three adult males of all-male group Brown B attempted to join group Yellow Prime. By the end of the mating season, these three males were fully integrated into the new group. After the group split, the two splinter groups still occupied the same home range but were never seen together.

DISCUSSION

This study is the beginning of a long-term research project in which we hope to continue to monitor the population of *L. catta* at Beza Mahafaly over many years. However, the results of the present report must be considered preliminary, since only 18 months are represented. During this short period of time, the population size remained stable, with a growth rate of 0.98. However, this was indeed a dynamic equilibrium. Changes occurring during the year included births, infant and adult deaths, male dispersal, and group fission. Adult sex ratios also changed within the population over the study period.

Population structure

Few primate populations studied to date have been found to be numerically stable (Dunbar, 1988). Many populations are declining because of natural climatic changes or human influences on their environment (e.g., Struhsaker, 1973; Mittermeier and Cheney, 1986). Other populations are increasing rapidly, usually due to provisioning or other human induced changes (e.g., Itani, 1975; Dunbar, 1980; Rasmussen, 1981; Sussman and Tattersall, 1986). If left to their own devices, many natural primate populations would probably exhibit alternating periods of growth and decline (see, e.g., Southwick and Siddiqi, 1977; Froelich et al., 1981; Winkler et al., 1984; Fishkind and Sussman, 1987).

Of course, the fact that the size of the ringtailed population at Beza Mahafaly was stable over a short period of time means very little. However, it is interesting to note that both prosimian populations censused at Berenty appear to be demographically stable. The sifaka (*Propithecus verreauxi*) population has changed little over 20 years (Richard, 1985), and the ringtailed population has remained remarkably stable for at least 15 years (Jolly et al., 1982; O'Connor, 1987). Are the riverine and xerophytic forests in which we find these populations more stable than other habitats in which primates have been studied? Do diurnal prosimians have a greater ability to maintain population stability than do anthropoids? If the prosimians are in a fine-tuned equilibrium with their environment, will slight perturbations cause major stress to these populations, as is indicated by the extremely low population density in the disturbed forest studied by O'Connor (1987)? Since the arrival of humans in Madagascar 1500–2000 years ago, at least 14 species of the lemur have become extinct. As yet, we do not know if the ringtailed lemur or sifaka populations at Beza Mahafaly are stable over long periods.

A number of investigators have found a relationship between population size and resource abundance. For example, Dunbar (1987) found a significant correlation, in black-and-white colobus monkeys, between group size and the total number of large trees. He speculates that the total number of large trees provides a better estimate of gross volume of food than does a simple measure of preferred food trees.

Terborgh (1986) has recently suggested that for any species there is an optimum group size, given the spatiotemporal dispersion of its major food resources, and that group size is thus relatively fixed within a species. Indeed, among *L. catta* in this study and at Berenty, group size did not differ significantly between habitats, but home range was closely correlated with the number of large trees within the range. Relationships between habitat quality and home range size have been established among a number of birds (e.g., Stenger Weeden, 1965; Holmes, 1970) and primates (e.g., Struhsaker, 1967; Takasaki, 1981).

Fertility and infant mortality

Ringtailed lemurs have a very high potential reproductive rate. Females begin to produce offspring by the second or third year (third year at Beza Mahafaly), and most females give birth every year thereafter. At Beza, the mean interbirth interval is 1.2 years, and age appears to be the major factor affecting fertility. Although social factors, such as a female's rank (e.g., Sade et al., 1976; Gouzoules et al., 1982; Wasser and Barash, 1983; Dunbar, 1984) or number of females in a group (Dunbar and Sharman, 1983; van Schaik, 1983), have been related to fertility in some primate populations, ringtailed females at Beza are generally successful in breeding each year. However, the fact that no twins were born at Beza Mahafaly and that females first give birth at age 3 years may indicate that there is some degree of environmental stress in this population (see, e.g., Altmann et al., 1988).

Age-specific fertility rates among the Beza Mahafaly ringtailed lemurs are similar to those of primates for which there are data available (see Dunbar, 1986) and for most mammals and birds (Caughley, 1966, 1977; Clutton-Brock, 1988). Fertility is low among young adult females and increases to a peak during physical prime, then declines at old age.

Infant mortality rates are relatively high both in the Berenty *L. catta* population and in that at Beza Mahafaly, with 52% of the infants dying in the first year in the latter site. At present we have too few data to discern any patterns in infant mortality. Around 20% of the infants born in 1987 and 1988 died within the first month. Infants also should be especially vulnerable to predation and other environmental stresses at 2.5–3 months of age when they begin to move independently and are being weaned, and perhaps during the peak of the dry season when they are 10–11 months old.

Patterns of adult mortality

A number of investigators have discovered relationships between adult mortality and environmental or social factors (Ohsawa and Dunbar, 1984; Teleki et al., 1976; Goodall, 1986), seasonal or periodic food shortages (Dittus, 1977; Otis et al., 1981; Milton, 1982; Hamilton, 1985), and predation (van Shaik and Hoof, 1983; Terborgh, 1986). Furthermore, many factors that cause mortality may have differential influences on individuals of different age, sex, or dominance status. For example, migrating males are assumed to be more susceptible to predation, nutritional stress, and agonistic attack (Dittus, 1977; Otis et al., 1981). Among females, reproduction and infant care are often stressful and mortality rates may be higher among individuals who are caring for young infants (Jolly, 1984; Sauther and Nash, 1987; Altmann et al., 1988; Richard and Rakotomanga, in press).

Thus knowledge of the patterns of mortality, such as age and sex of dying individuals and time of year of death, can often help us determine some of the possible causes. Among the ringtails at Beza Mahafaly, there are not enough data to speculate on the major factors influencing adult mortality, although the little evidence that exists fits some of the patterns described above. The one adult female found dead died, along with her infant, within a month of the infant's birth. The dead adult male was first missing from his group in January, 1988, and presumably was attempting to migrate. He was found on May 9, 1988, recently deceased, and there is evidence that he was the victim of predation by a fossa (*Cryptoprocta ferox*) or feral cat (Sauther, 1989). Furthermore, there is evidence that males in the process of migrating might be under nutritional stress. The three males of all-male group Brown B (the only males not members of a heterosexual group at the beginning of the 1988 period of male migration) weighed significantly less than all other adult males ($P < .001$, Student's t test). The average weight of all adult males was 2,213 g ($N = 41$, range 1,700–2,775), whereas the bachelor males weighed 1,700, 1,825 (the only adult males weighing less than 1,900 g), and 1,950 g. These three males were of three different adult age classes and all other adult males weighing less than 2,000 g ($N = 3$) were just reaching maturity. Loss of weight in transferring males has also been reported in toque macaques (Dittus, 1977).

Migration and group fission

In the majority of mammalian species investigated, and in most primates, males have a higher probability of leaving their natal group and of subsequent dispersal than do females (Greenwood, 1980; Pusey and Packer, 1986; Shields, 1987). *L. catta* shares this pattern of male-biased dispersal. Eight of the nine censused groups were affected by migration. In the ringtailed lemur, males leave of their own accord and are subject to agonistic attack mainly, but not solely, by the males of the group into which they are attempting to immigrate (Budnitz and Dainis, 1975; Jones, 1983; Sauther, in press). At Berenty, male migrations were observed around the birth season, whereas, at Beza, transfers occurred between December 26 (around the time infants were becoming independent) and the end of the mating season, May 31.

Although a number of investigators have discussed the possible benefits of transferring with group mates (see Pusey and Packer, 1986), in *L. catta* at Beza benefits did not seem to accrue to both partners equally. Kin selection has often been invoked as the reason for males to transfer together (Meikle and Vessey, 1981; van Noordwijk and van Schaik, 1985) and for males to transfer year after year into the same group (Colvin, 1983; Cheney and Seyfarth, 1983). However, since none of the partnerships at Beza Mahafaly were of similar-aged individuals, it is unlikely that these animals were closely related. Furthermore, since intergroup transfers were so frequent and complex, it seems unlikely that regular intergroup exchanges occur, although this remains to be seen.

At Berenty, most males transferred into groups with fewer males than the groups they had left. No simple pattern such as this emerged at Beza Mahafaly, with one exception. The two groups with the most skewed sex ratio (Yellow Prime and Blue) had the most individuals either immigrate or emigrate, and the direction of migration helped correct the imbalance. Furthermore, the number of males emigrating from the census population (11) was greater than that joining it (four), and this was a major factor in equalizing the sex ratio between the 1987 and 1988 birth season. Males at Berenty transferred into adjacent groups (although five of 17 were unaccounted for). The Berenty reserve is quite isolated from any other forest area. At Beza Mahafaly, most suspected transfer males that disappeared from the study area were not seen in nearby groups and migrating, collared males have been spotted in separate forests 2–3 km from the reserve.

The evolutionary or adaptive significance of migration has been discussed by a number of authors, as have the potential proximate causes (see Pusey and Packer, 1986; Shields, 1987; Dunbar, 1988; for reviews). In the ringtailed lemur, sexual competition and mate choice may be the driving force for male transfer. Migrations begin well before and culminate after the mating season. Resident males attempt to keep transferring males out of the group, and female choice is a prerequisite to mating success. Female ringtailed lemurs either allow males to approach them sexually or actively present to a male. Unacceptable males are rebuffed. In cases observed, resident central group males are allowed first access to receptive females. Females will also mate with peripheral males, with recently transferring males, and with males from adjacent, neighboring groups (Sauther, in press). Females reject advances of closely related males and possibly of unrelated natal males (Taylor and Sussman, 1985; Sauther, in press). Since central males appear to hold a favored position within groups, males may transfer into groups in which attaining this status seems more possible.

At the population level, the type of "trickle migration" (Dunbar, 1988) that occurs among *L. catta* appears to be important in smoothing out minor inequalities in sex ratios or in numbers of animals within groups as well as in randomizing gene flow. However, group fission may be more important than male transfer in adjusting population size over a larger area. If population growth occurs within one area, emigration of a splinter group, often to a less desirable habitat, may be a means of maintaining suitable population densities.

One group of ringtails did split at Beza Mahafaly. By the end of the study (almost a year after the initial fission), the two splinter groups still occupied the same home range, although one group seemed to be spending more time to the west of the reserve. Dunbar (1984, 1988) has speculated that groups of gelada baboons undergo fission because of social friction related to intrasexual competition. This "results in intolerable levels of harassment (and hence reproductive suppression through stress) for low-ranking females." (Dunbar, 1988: 84). It is interesting to note that the ringtailed group that split contained more adult females than any other group and yet had the lowest rate of fertility.

CONCLUSIONS

This study must be considered preliminary, since it covers less than the amount of time it takes for an infant *L. catta* to reach maturity. Our goal is to continue to monitor this population in the future and to expand the study to include some groups in unprotected areas outside of the Beza Mahafaly Reserve. Only with long-term research will we be able to determine how the environment influences population dynamics and how demographic variables affect and are affected by social organization. *L. catta* is listed in the IUCN Red Data book as not threatened, yet it appears that this species may be very sensitive to habitat quality and change. Although high population densities occur in gallery forests, ringtailed lemurs are found in much lower densities in dryer vegetation. Recent satellite photographs reveal that there are fewer than 1,000 ha of gallery forest remaining in southern Madagascar and that natural vegetation is disappearing rapidly in the south (G. Green, personal communication). *L. catta* does not respond well to human disturbance, and knowledge of the population structure and dynamics of this species is a prerequisite to its conservation.

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LITERATURE CITED

Altmann J, Altmann SA, and Haustfater G (1988) Determinants of reproductive success in savannah baboons (*Papio Cynocephalus*). In TH Clutton-Brock (ed): Reproductive Success. Chicago: University of Chicago, pp. 403–418.

Budnitz N (1978) Feeding behavior of *Lemur catta* in different habitats. Perspect. Ethol. *3:*85–108.

Budnitz N, and Dainis K (1975) *Lemur catta:* ecology and behavior. In I Tattersall and RW Sussman (eds): Lemur Biology. New York: Plenum, pp. 219–235.

Caughley G (1966) Mortality patterns in mammals. Ecology *47:*906–918.

Caughley G (1977) Analysis of Vertebrate Populations. New York: John Wiley.

Cheney DL, and Seyfarth RM (1983) Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. Am Naturalist *122:*392–412.

Cheney DL, Seyfarth RM, Andelman SJ, and Lee PC (1988) Reproductive Success in vervet monkeys. In TH Clutton-Brock (ed): Reproductive Success. Chicago: University of Chicago, pp. 384–402.

Clutton-Brock TH (1988) Reproduction Success. Chicago: University of Chicago.

Colvin J (1983) Influences of the social situation on male emigration. In RA Hinde (ed): Primate Social Relationships. Oxford: Blackwell, pp. 160–171.

Dittus WPJ (1977) The social regulation of population density and age-sex distribution in the toque monkey. Behaviour *63:*281–322.

Dunbar RIM (1980) Demographic and life history variables of a population of gelada baboons (*Theropithecus gelada*). J. Anim. Ecol. *49:*485–506.

Dunbar RIM (1984) Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies. Princeton, NJ: Princeton University.

Dunbar RIM (1985) Population consequences of social structure. In RM Sibly and RH Smith (eds): Behavioral Ecology: Ecological Consequences of Adaptive Behavior. Oxford: Blackwell.

Dunbar RIM (1986) Demography and reproduction. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham and TT Struhsaker (eds): Primate Societies. Chicago: University of Chicago, pp. 240–249.

Dunbar RIM (1987) Habitat quality, population dynamics, and group composition in colobus monkeys (*Colobus guereza*). Int. J. Primatol. *8:*299–329.

Dunbar RIM (1988) Primate Social Systems. Ithaca, NY: Comstock.

Dunbar RIM, and Sharman M (1983) Female competition for access to males affects birth rate in baboons. Behav. Ecol. Sociobiol. *13:*157–159.

Evans CS, and Goy RW (1968) Social behaviour and reproductive cycles in captive ringtailed-lemurs (*Lemur catta*). J. Zool. London *156:*181–197.

Fishkind AS, and Sussman RW (1987) Preliminary survey of the primates of the Zona Protectora and La Selva Biological Station, northeast Costa Rica. Primate Conserv. *8:*63–66.

Froehlich JW, Thorington RW Jr., and Otis JS (1981) The demography of howler monkeys (*Allouatta palliata*) on Barro Colorado Island, Panama. Int. J. Primatol. *2:*207–236.

Goodall J (1986) The Chimpanzees of Gombe. Cambridge: Belknap.

Gouzoules H, Gouzoules S, and Fedigan L (1982) Behavioural dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). Anim. Behav. *30:*1138–1150.

Greenwood PJ (1980) Mating systems, philopatry, and dispersal in birds and mammals. Anim. Behav. *28:*1140–1162.

Hamilton WJ (1985) Demographic consequences of a food and water shortage to desert chacma baboons, *Papio ursinus*. Int. J. Primatol. *6:*451–462.

Holmes RT (1970) Differences in population density, territoriality and food supply of dunlin on arctic and sub arctic tundra. In Watson A (ed): Animal Populations in Relation to Their Food Resources. Oxford: Blackwell, pp. 303–319.

Itani J (1975) Twenty years with Mt. Takasaki monkeys. In G. Bermant and DG Lindburg (eds): Primate Utilization and Conservation. New York: John Wiley, pp. 101–125.

Jolly A (1966) Lemur Behavior. Chicago: University of Chicago.

Jolly A (1972) Toop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatol. *17:*335–362.

Jolly A (1984) The puzzle of female feeding priority. In M Small (ed): Female Primates: Studies by Woman Primatologists. New York: Alan R. Liss, Inc., pp. 197–215.

Jolly A, Oliver WLR, and O'Connor SM (1982) Population and troop ranges of *Lemur catta* and *Lemur fulvus* at Berenty, Madagascar: 1980 census. Folia Primatol. *39:*115–123.

Jones KC (1983) Inter-troop transfer of *Lemur catta* at Berenty, Madagascar. Folia Primatol. *40:*145–160.

Meikle DB, and Vessey SH (1981) Nepotism among rhesus monkey brothers. Nature *294:*160–161.

Mertl-Millhollen AS, Gustafson HL, Budnitz N, Dainis K, and Jolly A (1979) Population and territory stability of the *Lemur catta* at Berenty, Madagascar. Folia Primatol. *31:*106–122.

Milton K (1982) Dietary quality and demographic regulation in a howler monkey population. In EG Leigh, AS Rand, and DM Windsor (eds): The Ecology of a Tropical Forest. Washington, DC: Smithsonian, pp. 273–289.

Mittermeier RA, and Cheney DL (1986) Conservation of primates and their habitats. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds): Primate Societies. Chicago: University of Chicago, pp. 477–490.

O'Connor SM (1987) The Effect of Human Impact on Vegetation and the Consequences to Primates in Two Riverine Forests, Southern Madagascar. PhD Thesis, University of Cambridge.

Ohsawa H, and Dunbar RIM (1984) Variations in the demographic structure and dynamics of gelada baboon populations. Behav. Ecol. Sociobiol. *15:*231–240.

Otis, JS, Froehlich JW, and Thorington RW Jr. (1981) Seasonal and Age-related differential mortality by sex in the mantled howler monkey, *Alouatta palliata.* Int. J. Primatol. *2:*197–205.

Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis.* Anim. Behav. *27:*1–36.

Pusey AE, and Packer C (1986) Dispersal and philopatry. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds): Primate Societies. Chicago: University of Chicago, pp. 250–255.

Rasmussen DR (1981) Communities of baboon troops (*Papio cynocephalus*) in Makumi National Park, Tanzania. Folia Primatol. *36:*232–242.

Ratsirarson J (1987) Contribution a l'Etude Comparative d l'Ecoethologie de *Lemur catta* dans Deux Habitats Differents de la Reserve Speciale de Beza Mahafaly. Memoire de fin d'Etudes, Universite de Madagascar, Tananarive.

Richard AF (1985) Primates in Nature. New York: Freeman.

Richard AF, and Rakotomanga P (in press) Demography of *Propithecus Verreauxi* at Beza Mahafaly: I. sex ratios and life table, 1984–1988. Am J. Phys. Anthropol.

Richard AF, Rakotomanga P, and Sussman RW (1987) Beza Mahafaly: recerches fondamentales et appliquees. In RA Mittermeier, LH Rakotovao, V Randrianasolo, EJ Sterling, and D Devitre (eds): Priorites en Matiere de Conservation des Especes a Madagascar. Gland: IUCN, pp. 45–49.

Sade DS, Cushing K, Cushing P, Dunaif J, Figueroa A, Kaplan J, Lauer C, Rhoades D, and Schneider J (1976) Population dynamics in relation to social structure on Cayo Santiago. Yearb. Phys. Anthropol. *20:*253–262.

Sauther ML (in press) Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Am. J. Phys. Anthropol.

Sauther ML (1989) Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Int. J. Primatol. 10:595–606.

Sauther ML, and Nash LT (1987) Effect of reproductive state and body size on food consumption in captive *Galago senegalensis braccatus.* Am J. Phys. Anthropol. *73:*81–88.

Shields WM (1987) Dispersal and mating systems: investigating their causal connections. In BD Chepko-Sade and ZT Halpin (eds): Mammalian Dispersal Patterns. Chicago: University of Chicago, pp. 3–24.

Southwick CH, and Siddiqqi MF (1977) Population dynamics of Rhesus monkeys in northern India. In HSH Prince Ranier III and G. Bourne (eds): Primate Conservation. New York: Academic, pp. 339–362.

Stearns SC (1977) The evolution of life history traits. Annu. Rev. Ecol. Syst. *8:*145–171.

Stenger Weeden J (1965) Territorial behaviour of the tree sparrow. Condor *67:*193–209.

Struhsaker TT (1967) Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli game reserve, Kenya. Ecology *48:*891–904.

Struhsaker TT (1973) A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. Ecology *54:*930–932.

Strum SC, and Western JD (1982) Variations in fecundity with age and environment in olive baboons (*Papio anubis*). Am. J. Primatol. *3:*61–76.

Sussman RW (1974) Ecological distinctions in sympatric species of *Lemur.* In RD Martin, GA Doyle and AC Walker (eds): Prosimian Biology. London: Duckworth, pp. 75–108.

Sussman RW, and Rakotozafy A (in preparation) Diversity and density of the vegetation in the Beza Mahafaly Special Reserve, southern Madagascar.

Sussman RW, and Tattersall I (1986) Distribution, abundance, and putative ecological strategy of *Macaca fascicularis* on the Island of Mauritius, southwestern Indian Ocean. Folia Primatol. *46:*28–43.

Takasaki H (1981) Troop size, habitat quality and home range area in Japanese macaques. Behav. Ecol. Sociobiol. *9:*277–281.

Tattersall I (1982) The Primates of Madagascar. New York: Columbia University.

Taylor L (1986) Kinship, Dominance, and Social Organization in a Semi-free Ranging Group of Ringtailed Lemurs (*Lemur catta*). PhD dissertation, Washington University, St. Louis.

Taylor L, and Sussman RW (1985) A preliminary study of kinship and social organization in a semi free-ranging group of *Lemur catta.* Int. J. Primatol. *6:*601–614.

Teleki G, Hunt EE Jr., and Pfifferling JH (1976) Demographic observations (1963–1973) on the chimpanzees of Gombe National Park, Tanzania. J. Hum. Evol. *5:*559–598.

Terborgh J (1986) The social systems of New World primates: an adaptionist view. In JG Else and PC Lee (eds): Primate Ecology and Conservation. Cambridge: Cambridge University. pp. 199–211.

Van Horn RN, and Resko JA (1977) The reproductive cycle of the ring-tailed lemur (*Lemur catta*): Sex steroid levels and sexual receptivity under controlled photoperiods. Endocrinology *101:*1579–1586.

van Noordwijk MA, and van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim. Behav. *33:*849–861.

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour *87:*120–144.

Wasser SK, and Barash DP (1983) Reproductive suppression among female mammals: Implications for biomedicine and sexual selection theory. Q. Rev. Biol. *58:*513–538.

Winkler P, Loch H, and Vogel C (1984) Life history of hanuman langurs (*Presbytis entellus*): Reproductive parameters, infant mortality and troop development. Folia Primatol. *43:*1–23.