Demographic and Life-History Patterns in a Population of Ring-Tailed Lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-Year Perspective

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ABSTRACT Over 15 field seasons (1987–2001), we collected census and life-history data on a population of individually identified ring-tailed lemurs at the Beza Mahafaly Reserve, Madagascar. No significant difference was found in population size over the study period, though a marked decline in the population occurred following a 2-year drought. The population rebounded rapidly after the immediate postdrought period. There was nearly a complete replacement of individuals over the study period. Average group size is 11.5 animals, and adult male to female sex ratio is 0.92. Most females reproduce annually, and the average fecundity rate is 84.3%. The greatest variability in fecundity is found among old females. We suggest that ring-tailed lemur females follow an "income breeding" strategy, i.e., females use maximum resources during reproduction rather than relying on fat stores, as do "capital breeders." Infant mortality to 1 year of age in a nondrought year is 52%, higher than infant mortality in small to medium-sized anthropoids. The oldest known female was 18 years old in 2001. We suggest that 18–20 years may represent the maximum life-span for wild ring-tailed lemurs. Because males regularly emigrate from the population, we have no data regarding male life-span; however, there is some indication that males do not survive as long as females. Group fission has occurred three times: twice from one parent group living in the driest area of the reserve, with the most dispersed food resources. We suggest that the reproductive strategy that has evolved in this species, wherein females reproduce early in life and annually until old age, is a response to the unusual climate and environmental conditions under which *Lemur catta* has evolved. Am J Phys Anthropol 120: 182–194, 2003. © 2003 Wiley-Liss, Inc.

While Malagasy lemur population patterns and life-histories were largely unknown in the early decades of primate research, several demography and life-history studies during the past decade indicate considerable variability in lemur reproductive strategies and adaptive responses to both natural conditions and stochastic events (Sussman, 1991; Richard et al., 1991, 2002; Wright, 1995; Johnson and Overdorff, 1999; Overdorff et al., 1999; Jolly and Pride, 1999; Koyama et al., 2001; Atsalis, 2000; Jolly et al., 2002).

In her review of lemur life-history traits and their correlation to Madagascar's environment, Wright (1999) suggests that many of the characteristics considered unique to lemurs, e.g., female dominance, targeted female-female aggression, high infant mortality, strict seasonal breeding, and weaning synchrony, have arisen as a response to Madagascar's harsh and unpredictable island environment. Wright (1999) argues that these traits can be seen as adaptations to conserve energy and maximize the use of scarce resources in such a situation.

Sussman (1991) stressed that only with long-term research on wild primate populations can we begin to determine how the environment influences population dynamics, as well as understand the relationship between demographic variables and social organization. Furthermore, long-term life-history studies on primates are relatively uncommon, largely due to slow growth rates in terms of both

body mass and brain size, variables which result in what Richard et al. (2002) refer to as "life in the slow lane."

To determine how Madagascar's unique environment influences the life-history of the ring-tailed lemur (*Lemur catta*), we present here the results of a long-term demographic and life-history study on a population of ring-tailed lemurs at the Beza Mahafaly Special Reserve, southwestern Madagascar, using data accumulated between 1987–2001. We make comparisons with another population of ring-tailed lemurs that has been studied at Berenty Reserve, a different site, for 33 years (Jolly et al., 2002) and 10 years (Koyama et al., in press), and we also present some life-history comparisons with a population of white sifaka (*Propithecus verreauxi*), which are sympatric with the *Lemur catta* at Beza Mahafaly, and which have been the focus of a 16-year study (Richard et al., 2002). Furthermore, we discuss how ring-tailed lemur life-history patterns found at Beza Mahafaly relate to climatic variables that are specific to southwestern Madagascar.

SPECIES BACKGROUND, RESEARCH SITE, STUDY ANIMALS, AND METHODS

The behavior and ecology of the ring-tailed lemur (*Lemur catta*) have been studied extensively in the wild at three Madagascar sites: Berenty Reserve in the far south of the island (Jolly, 1966, 1972; Jolly et al., 1982, 1993, 2000, 2002; Jolly and Pride, 1999; Sussman, 1974, 1977; Gould, 1990; Koyama, 1988, 1991; Koyama et al., 2001, in preparation; Nakamichi and Rakototiana, Koyama et al., 1997; Nakamichi and Koyama, 1997; Hood and Jolly, 1995; Rasamimanana and Rafidinarivo, 1993), at Beza Mahafaly in the southwest (Sussman, 1991, 1992; Sauther, 1989, 1991, 1992, 1993, 1998; Sauther et al., 1999, 2002; Gould, 1994, 1996a,b, 1997a,b, 2000; Gould et al, 1999), and at Antserananomby in Western Madagascar (Sussman, 1972, 1974, 1977). Sauther et al. (1999) present a comprehensive review of *Lemur catta* socioecology.

Characteristics of *Lemur catta* which have been discussed elsewhere (see above references), and which are important to the understanding of the present study, include: female philopatry; marked female dominance in all feeding and social contexts; short and discrete mating, birth, and lactation seasons, with simultaneous lactation by all females in a population during the height of the dry season; and rapid growth rate of infants, in relation to maternal body size.

Beza Mahafaly Reserve is situated in southwestern Madagascar, 23° 30′ S. latitude and 44′ E. longitude (Fig. 1). It was established as a Special Government Reserve in 1986 (Richard et al., 1987). Parcel 1 of this reserve, where the study took place, consists of 80 ha of mixed vegetation: riverine forest in the eastern part of the reserve, near the Sakamena River, and more xerophytic forest as one

moves to the western boundary (Sussman and Rakotozafy, 1994).

Home range sizes of nine groups of ring-tailed lemurs living in the reserve were determined by Sussman (1991). Groups whose home ranges are in the eastern riverine forest section of the reserve, bordering on the Sakamena River, had an average home range size of 17 ha. Home ranges of groups residing in the drier and more vegetation-sparse central and western part of the reserve averaged 32 ha.

Between 1987–1995, all subadult (2-year-old) and adult ring-tailed lemurs residing in the nine social groups within the reserve boundaries (and one adjacent group) were captured by R.W.S. and M.L.S. and fitted with nylon collars and numbered plastic tags for individual identification. In 2001, all adult males in three of the groups were captured and collared by L.G. for identification in a hormonal study (in progress). The collar color indicates to which group the animal belongs. The nine original groups were given the following names: Red, Green, Blue, Black, Tan East, Tan West, Yellow, Yellow Prime, and Brown. The animals were darted using a Telinject blowpipe and tranquilized with either 2 cc of ketamine chloride between 1987–1995, or 0.25–0.30 cc of Tiletamine (Telazol) in 2001.

While animals were immobilized, the following information and samples were obtained: weight, reproductive state, general physical condition, internal body temperature, heart rate, hair samples, and dental examination (all years), and between 1987–1995, dermatoglyphs, fecal samples, body measurements, and dental casts.

Relative age-classes of each captured animal were determined by a set of dental-wear criteria developed by M.L.S. and R.W.S. The age-classes used in this study (subadult, young adult, prime, and old) are based on the following criteria. For assignment into age grades, all criteria had to apply. Subadults had weights less than 1,400 g, upper canines that were not fully erupted (upper canines are the last to erupt in *L. catta*; Schwartz, 1974; Eaglen, 1985), overall dental attrition scores of 1.00 (see below), little to no wear on occlusal surfaces, no dentin exposure for any teeth, undescended testicles for males, and nipples that were <0.5 cm in length for females. Young adults had fully erupted canines, weights greater than 1,400 g but less than 2,000 g, overall dental attrition scores that were >1.00 but <1.50, some teeth that exhibited small wear facets but no dentin exposure, small but descended testicles for males, and nipples that were >0.5 cm in length for females. Prime-aged individuals had weights greater than 2,000 g, overall dental attrition >1.5 but <2.5, large wear facets on most teeth and small dentin exposure only at the cusps, large and fully descended testicles for males, and female nipples that were >0.5 cm in length. Old individuals had weights that were greater than 2,000 g, nipples that were >0.5 cm in length for females, overall
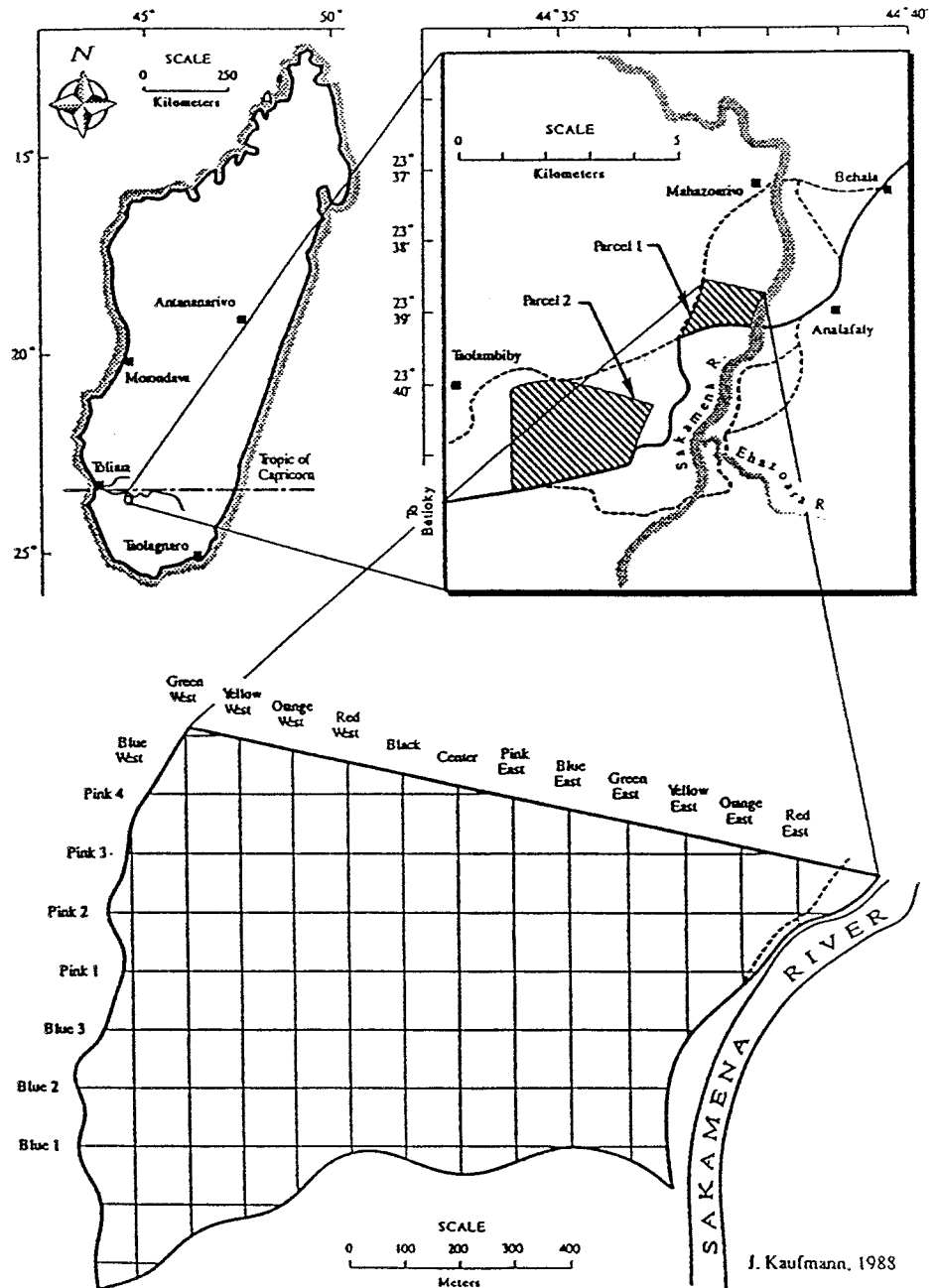
Fig. 1. Trail map and geographical location of Beza Mahafaly Special Reserve, Madagascar.

dental attrition scores that were >2.5, no original cusps that remained, and at least one molar tooth that was worn to the point of actual pulp exposure.

Censuses were conducted annually (and in some years, more frequently) between 1987–1996, and again between 1999–2001 by either the authors or field assistants. When each study group was located, all adult animals were counted and sexed, and juveniles and infants (if present) were counted. Tag numbers were noted. Number and sex of uncollared adults were also recorded. For the years 1987–1989, 1992, 1994, and 1996, we have data on the number of females actually giving birth. For all other years, the data reflect females who produced surviving infants.

In this paper, total fecundity rate is the number of females observed with an infant relative to the total number of females in that age category during that year.

RESULTS

Population changes

Between 1987–1995, 150 adult ring-tailed lemurs were collared and tagged in the Beza Mahafaly Reserve population over 4 different years of collaring (1987, 1988, 1990, and 1995). In 2001, only 12 (8%) of these collared animals remained in the population. Only one animal, a female, collared in the first year of the study, was present in 2001, as well as 3
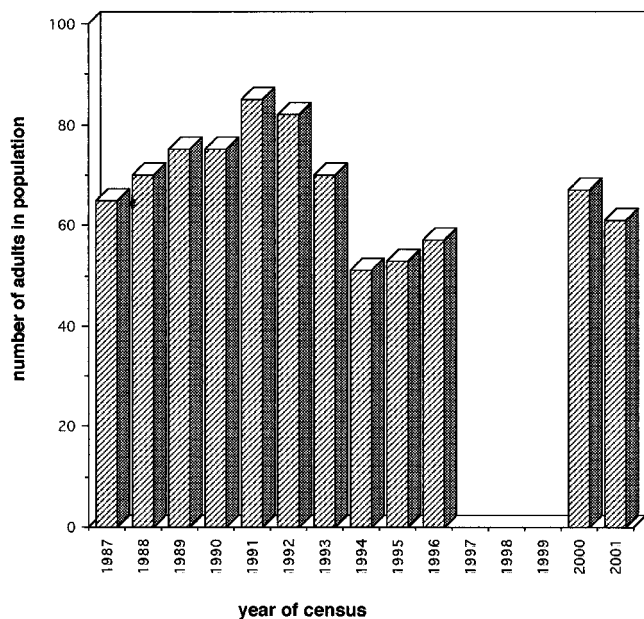
Fig. 2. Number of adult ring-tailed lemurs in the Beza Mahafaly population, 1987–2001. Censuses were not conducted between 1997–1998. In 1999, adults and subadults were not differentiated; thus, the data could not be used.

Fig. 3. Noninfant population of ring-tailed lemurs in the Beza Mahafaly population, 1987–2001. Censuses were not conducted in 1998 and 1999.

animals (female) collared in 1990 and 8 (5 females, 3 males) from the 1995 collaring. The last of the 62 adult males collared in the early years of the study (1987–1990) disappeared in 1999.

No significant difference was found in adult population size over the study period ($\chi^2 = 18.9$, df = 11, Fig. 2) or total population excluding infants but including subadults (1- and 2-year-old, $\chi^2 = 18.1$, df = 12, Fig. 3).

There was, however, a marked decline in the adult population of 1994, 1995, and 1996, and in the noninfant population of 1994 and 1995, following a severe drought in the region (Gould et al., 1999). The population has since recovered slowly, and the number of animals censused in 2001 (adult n = 61 and noninfant population n = 102) is similar to that found in the first year of the study (adult n = 65 and noninfant population n = 107). However, while the number of *Lemur catta* living in the reserve in 2001 is similar to that of 1987, there has been almost a complete replacement of actual individuals.

Group size

Over the course of the study, group size ranged from 2–15 adults, and average adult group size was 8.2 (N = 85 groups). When juveniles (1- and 2-year-olds) are included, group size ranged from 3–21 animals, with an average of 11.5 (N = 85 groups). Average group sizes for years 1, 5, 10, and 15 of the study are presented in Table 1.

Sex ratio

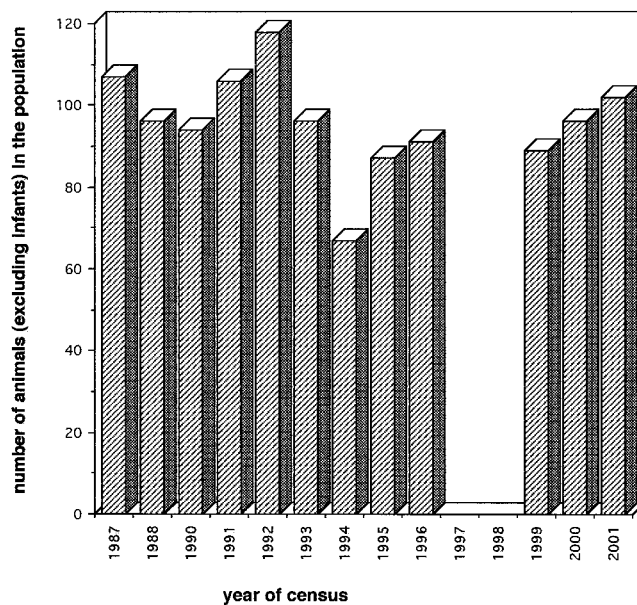Male-to-female sex ratio was calculated for years 1, 5, 10, and 15 of the study (Table 1). In 1987 and

1996, sex ratio was biased in favor of males, though in 1996 it was nearly even. In the other 2 years, 1991 and 2001, there were more females than males living in the reserve population. Overall adult male-to-female sex ratio for all years in which censusing was conducted is 0.92.

Total female fecundity

We have total female fecundity rates for 6 of the 15 years that demographic data were collected (Table 2). Most females gave birth in most years, although we found that in both 1992, the second year of the drought, and 1994, when the population decline from the drought was at its peak, fewer females gave birth. The average total fecundity rate is 84.3%.

Table 3 summarizes age-specific fecundity rates for the 6 years. Predictably, the age-category responsible for the majority of births, which is also the most stable age-category in terms of fertility rate, is the prime category, particularly the younger females in this category. Fertility rates for young adult females are relatively variable (0.60–1.00), but the old female category exhibits the most marked variation, ranging from 0.29–1.00.

Births and number of females in group

It was possible to calculate number of births per number of females in a group for 5 nondrought years, 1987, 1988, 1989, 1994, and 1995. As might be expected, mean number of births increased as number of females in a group increased; however, number of births began to fall when number of females in a group reached 6 and 7, respectively (Fig. 4).

Number of females in groups ranged from 1–7 during the above-mentioned years. The modal num-

TABLE 1. *Group structure of* Lemur catta *population at Beza-Mahafaly, 1987, 1991, 1996, and 2001*

Year of census	1987	1991	1996	2001
No. of groups	8.0	9.0	8.0	9.0
Mean group size	12.0	11.3	11.5	11.0
Mean no. of adult females	3.6	5.6	4.1	4.0
Mean no. of adult males	4.5	4.2	4.2	3.2
Mean no. of immatures (excluding infants)	3.8	2.9	3.1	3.2
Adult M/F ratio	1.34	0.80	1.03	0.82

TABLE 2. *Birth rates*
(based on data collected over 6 birth seasons)

Birth season year	Proportion of females giving birth	Percentage of females giving birth
1987	24/27	89%
1988	27/34	79%
1989	31/36	86%
1992[1]	29/39	74%
1994	28/28	100%
1996	25/32	78%
Average birth rate, 84.3%		

[1] Second year of a 2-year drought.

ber of females per group was 4 (number of groups considered = 40; Fig. 5).

Habitat differences do not appear to affect the number of females residing in a group, as no significant differences were found in number of females per group in groups with home ranges in the xerophytic/scrub area of the reserve vs. the riverine forest area (Table 4).

Infant mortality

Infant mortality at 1 month of age was recorded for 1987 (20%), 1988 (18%), and 1992 (63%). Three-month mortality was 77% in 1992, but only 16% in 1996. The unusually high percentages of 1- and 3-month mortality occurred in 1992, at the end of the 2-year drought period. Infant mortality over an entire year was 52% in 1987/1988 and 80% during the 1992/1993 drought and immediate postdrought period (Table 2). The most likely average infant mortality to 1 year of age in a nondrought year is around 50%.

Juvenile (one-year) survivorship

In 1988 and 1989, survivorship of yearlings was 48% and 46%, respectively. In both 1990 and 1995, censuses were collected when juveniles were 8 months of age. At 8 months, survivorship was predictably higher, at 67% and 83%, respectively.

Female life-span

The total number of adult females collared and tagged in the initial 3 years of the study (1987–1990) was 52, and in 1995, 18 females were marked for identification. We also know true ages for the animals that were collared as subadults (2-year-olds) or young adults (3–4 years). In 2001, 5 of the adult females collared in the initial 3-year period were still residing in the reserve population. Their ages in 2001 were 13, 14, 16, 16, and 18. Another female that died in 2000 was 16 years of age. Very few females survive to these ages, as the majority of the females (73%) collared between 1987–1990 had disappeared by 1995, and of the 18 females collared in 1995, 72% were missing from the 2001 census.

Male life-span

The last of the 62 adult males that were collared between 1987–1990 disappeared from the reserve population in 1999. Of the 18 adult males collared in 1995, only 3 resided in the reserve population in 2001. In 2000 and 2001, line-transect surveys were conducted approximately 1 km north and south of the reserve boundaries, and in 2000, 2 males collared in 1995 were found living in groups approximately 1 km south of the reserve, and none to the north. In 2001, only one male was seen in one of the groups to the south (Sauther and Whitelaw, personal communication).

Group fission, dissolution, and formation of new groups

Over the 15-year period, one group residing in the driest part of the reserve (Yellow Group) fissioned twice, and in 2000, Brown Group, living partly in the reserve and partly adjacent to the researcher's camp, fissioned. When Yellow Group fissioned for the first time, it contained 18 individuals. After the split, the fissioned group, Yellow Prime, contained 4 members from Yellow Group plus 3 migrating males. Between 1996–1999, a second fission occurred, with 3 females and 2 males breaking off from the original Yellow Group, forming Yellow Three. In 1999, Brown Group, residing in and around the researcher's camp and along the south-central border of the reserve, fissioned. These two groups are now referred to as Brown One and Brown Two. Over the 15-year study period, this group had experienced the largest range in membership, from a low of 13 to a maximum of 23, with an average size of 17 animals. Although the number of animals living in the group in 1998, the year before the split, is unknown, in 1999, only one of the subgroups was seen, composed of just 5 individuals. In 2001, both subgroups were counted, and consisted of 8 and 6 animals each. Home ranges of all fissioned groups are either identical to the parent group (but the two groups rarely utilize the same areas at the same time), or the fissioned group uses part of the parent group's home range, and extends its own range from the boundaries of the parent group's range (Fig. 6).

TABLE 3. Number of births by age-category of female and fertility rate by age-category[1]

Age-class of female	1987	1988	1989	1992	1994	1996
Young adult (3–4 years)	4 (4)	6 (8)	12 (15)	8 (13)	8 (8)	3 (5)
	FR = 1.00	FR = 0.75	FR = 0.80	FR = 0.62	FR = 1.00	FR = 0.60
Young prime (5–8) and prime (9–12)	15 (16)	18 (19)	12 (14)	19 (19)	18 (18)	20 (24)
	FR = 0.94	FR = 0.95	FR = 0.86	FR = 1.00	FR = 1.00	FR = 0.83
Old prime and old (13+)	5 (7)	3 (7)	7 (7)	2 (7)	2 (2)	2 (3)
	FR = 0.71	FR = 0.43	FR = 1.00	FR = 0.29	FR = 1.00	FR = 0.66

[1] Number of births is first number in each cell, total number of females in each age-category is in parentheses beside total number of births. FR, fertility rate for each age-category. The term "age-category" is used here, as some age-classes have been combined because actual ages were not known for each female, i.e., some females were designated as "young prime/prime" or "old prime/old."
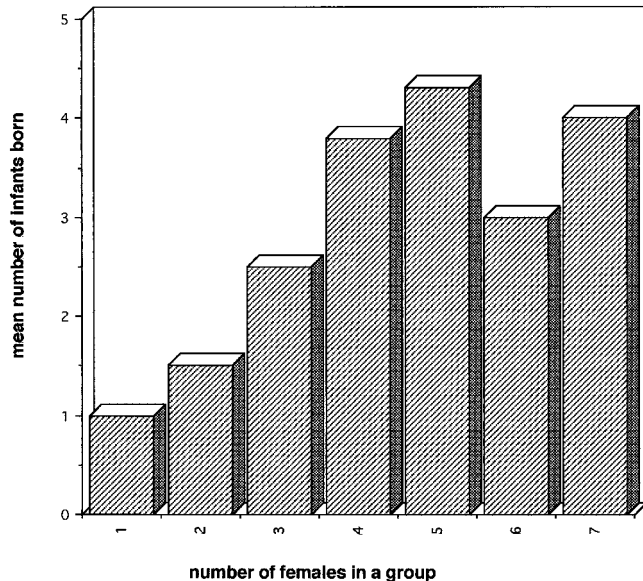

Fig. 4. Mean number of infants born to groups containing differing numbers of adult females.

Fig. 5. Number of females per group in a sample of 40 groups over the study period. Modal number of females per group was 4.

With some group fissions, a pair or small subgroup of females has been forced out of the larger parent group, and over time, these females acquire males and eventually establish a home range. Lone females or pairs of females, sometimes with juveniles, have occasionally been observed on their own in the reserve. These females have either been expelled from their groups, or their group has dissolved. If these females attempt to join an established group, they usually become the targets of marked aggression by resident females and are repelled. One pair of such females, whose own group (Blue) no longer existed, was observed in 1994 by L.G. They were continually chased to the periphery of Green Group (the group they were attempting to join), and a resident female of the Green Group attempted to kill the infant of one of the peripheral females. The two peripheral females eventually established a group of their own (see below). However, not all lone females or pairs of females are as successful, and some have simply disappeared.

Three of the original groups, Blue, Black, and Tan West, no longer exist. One new group formed in 1995, composed of females formerly from Blue and Black Groups, as well as some dispersing males.
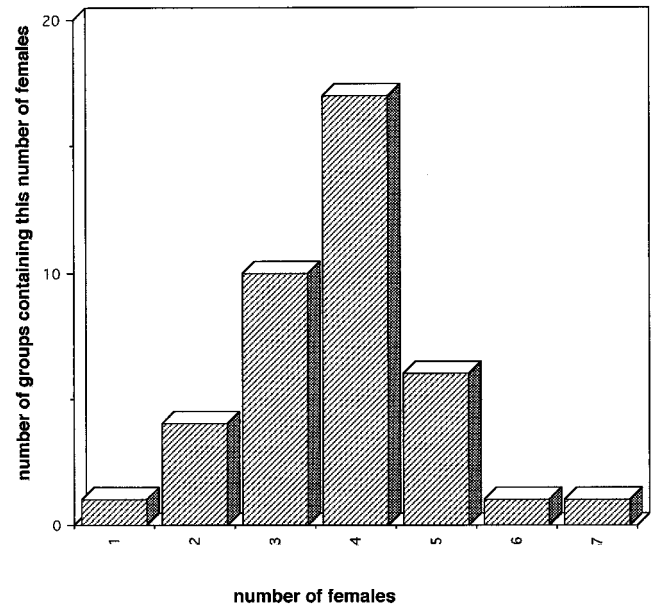
This new group, named Lavender, now has a firmly established home range in the most densely populated area of the reserve.

DISCUSSION

Population changes and population stability

Demographic studies of naturally occurring primate populations over the past three decades have revealed a great deal of variation in population structure. In many studies, a steady increase in population has been noted (geladas, Dunbar, 1980; capuchins, Fedigan et al., 1996; muriquis, Strier et al., 1993; moor macaques, Okamoto et al., 2000; rhesus, long-tailed, and Tibetan macaques, Wong and Ni, 2000; ring-tailed lemurs at Berenty reserve, Jolly et al., 2002; Koyama et al., in press), while other populations have decreased, sometimes dramatically (vervet monkeys, Struhsaker, 1973, Struhsaker, 1976; chacma baboons, Hamilton, 1985; Toque macaques, Dittus, 1988; Barbary macaques, Ménard and Vallet, 1996; Sulawesi crested black macaques, Rosenbaum et al., 1998; yellow baboons, Rhine et al., 2000; black and white ruffed lemurs, Ratsimbazafy, 2002).

TABLE 4. *Number of females per group in groups residing in xerophytic/scrub forest vs. riverine forest areas of reserve in years 1, 5, 10, and 15 of study (1987, 1991, 1996, and 2001)*[1]

Xerophytic/scrub forest number of females per group	Riverine forest number of females per group
1987	1987
Yellow 1 N = 5	Red N = 3
Yellow 1 N = 3	Green N = 5
Tan West N = 4	Blue N = 3
	Black N = 4
	Brown N = 6
	Tan East N = 5
1991	1991
Yellow 1 N = 8	Red N = 3
Yellow 2 N = 7	Green N = 7
Tan West N = 4	Blue N = 3
	Black N = 6
	Brown N = 8
	Tan East N = 4
1996	1996
Yellow 1 N = 8	Red N = 4
Yellow 2 N = 4	Green N = 5
Tan West N = 1	Blue no longer exists
	Black no longer exists
	Brown N = 6
	Tan East N = 4
	Lavender (new group) N = 2
2001	2001
Yellow 1 N = 4	Red N = 4
Yellow 2 N = 4	Green N = 5
Yellow 3 N = 4	Brown 1 N = 6
Tan West no longer exists	Brown 2 N = 4
	Tan East: not possible to count individual females, only total number of adults
	Lavender N = 4

[1] No significant differences were found when comparing females per group in the two diverse areas in any of the above years ($P > 0.05$).

Explanations for both declines and increases in primate populations are related to a great variety of both natural and human-induced variables. For example, of the studies cited above, population decreases have been attributed to hunting pressure and habitat loss (Rosenbaum et al. 1998), natural reduction in food resource availability due to a rising water table and salt layer in Amboselli Park (Struhsaker, 1973), droughts (Hamilton, 1985; Dittus, 1988), postcyclone damage (Dittus, 1988; Ratsimbazafy, 2002), fruiting failures (Tutin et al., 1997; Jolly et al., 2002), food competition and predation (Rhine et al., 2000), and caterpillar plagues which affected abundance of available food (Ménard and Vallet, 1996). Population increases have occurred in situations of low predator pressure, absence of hunting, absence of habitat loss (Strier et al., 1993), regenerating and increasing habitat (Fedigan et al., 1996), or water and controlled food provisioning (Jolly et al., 2002; Koyama et al., in press).

We found a marked decline in the adult ring-tailed lemur population at Beza Mahafaly between 1994–1996, and in the noninfant population between 1994–1995. These were years following a severe 2-year drought in the region which seriously affected the availability of key resources in the reserve. The consequences of the drought are discussed in detail in Gould et al. (1999). The population in nondrought or immediate postdrought years, however, appears to stabilize at about 60–70 adults and 100–110 animals when immatures (excluding infants) are considered.

Line-transect censuses were conducted 1 km north and 1 km south of the reserve along the eastern (riverine) border in 2001 by Whitelaw and Sauther. Although these forest areas are continuous with the riverine forest in the Beza Mahafaly reserve, they are highly degraded, primarily due to cattle and goat grazing and firewood collection. Whitelaw and Sauther found three groups to the north of the reserve, totalling 25 animals, and two groups to the south, also totalling 25 animals (Whitelaw, personal communication). Comparatively, a 1-km transect within the Beza Mahafaly reserve boundary at the eastern riverine border yielded a total of four groups and 52 animals. Thus, ring-tailed lemur density within the reserve, at least at the eastern, riverine edge, is double that found outside of the reserve. The population residing within the reserve boundaries may reflect the optimum carrying capacity for this species in a relatively undisturbed 80-ha patch of deciduous/xerophytic forest in this geographic region.

Group size difference in two ring-tailed lemur populations

Sibley (1983) argues that optimal group size is unstable, and that groups tend to be greater than optimal size. Jolly et al. (2002) suggest that the *Lemur catta* population at Berenty reserve in southern Madagascar, a population in which some groups experience water and controlled food provisioning, fits with the argument of Sibley (1983) concerning group size remaining suboptimally large, because the cost of fissioning to smaller groups would be too great. However, Koyama et al. (2001), working in the tourist area of Berenty reserve, where more provisioning occurs and population density is greater, notes frequent fissioning. Group size at Berenty is higher in tourist/provisioning areas than that found at Beza Mahafaly. Jolly et al. (2002) report 12.4–14 animals per group, and Koyama et al. (in press) report a mean of 16 animals in the most heavily provisioned "tourist" areas of Berenty, whereas in the scrub forest area, where provisioning does not occur, mean group size (9.2) is similar to our mean group size at Beza Mahafaly (11.5). When group size at Beza Mahafaly reaches a critical number (approximately 14–21 individuals; particularly with respect to groups living in the drier area of the reserve), they fission into two smaller groups. The benefits of fissioning must outweigh the costs, since it has occurred three times in the past decade, and all fissioned groups are still present in the population. Thus, group size at Beza Mahafaly does not seem to fit with the suggestion by Sibley (1983) that group size should be suboptimally large. However, small to
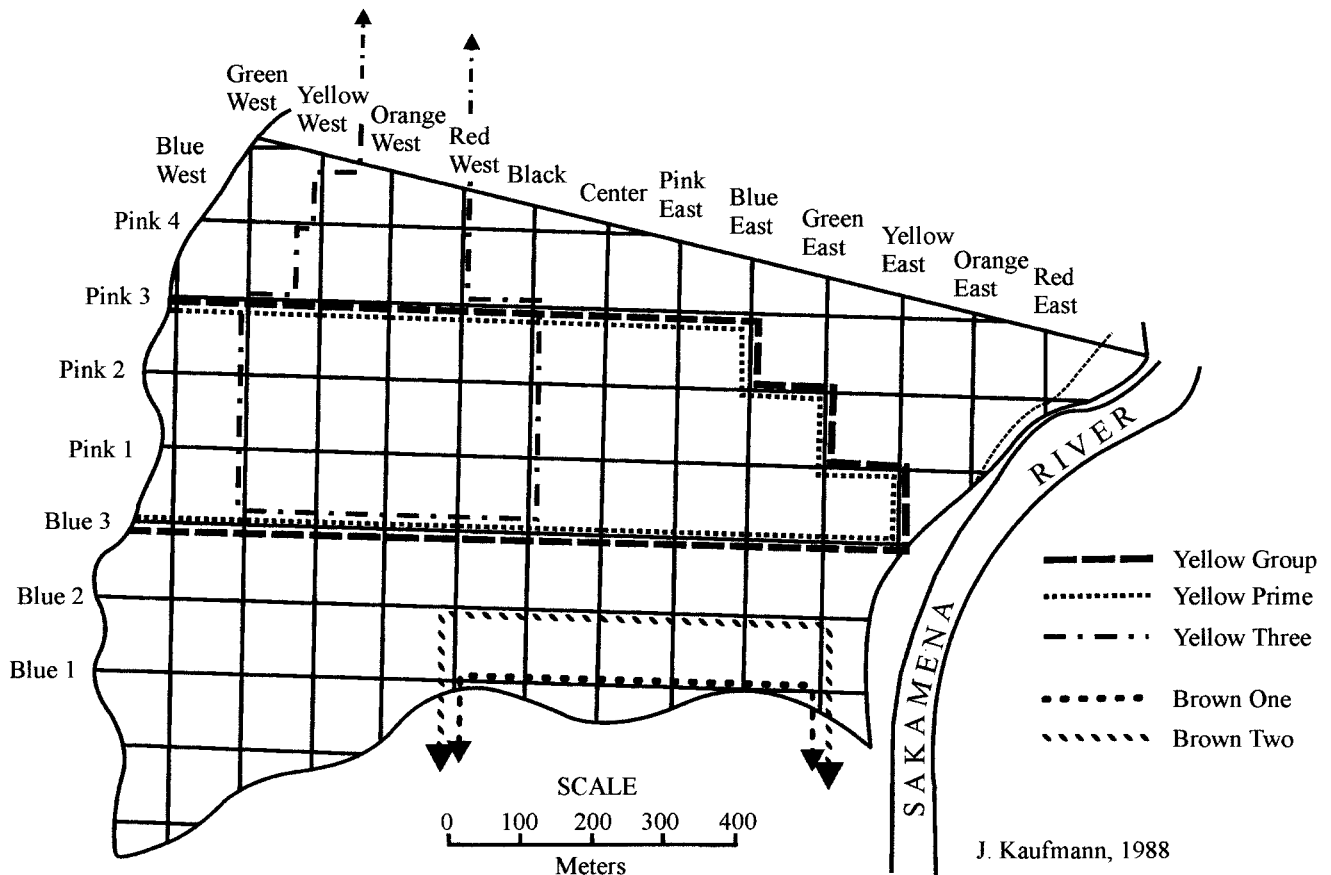
Fig. 6. Home ranges of parent groups Yellow Group and Brown One, and the groups which fissioned from these: Yellow Prime and Yellow Three, and Brown Two.

very small groups (<6) are at the greatest disadvantage in terms of frequent displacement at feeding sites by larger groups in overlapping areas of the home range, so the prediction of Sibley (1983) that small groups are at a distinct disadvantage in terms of maximizing individual fitness could be applied here.

Female fecundity and birth rates by age-category

Mean fecundity at Beza Mahafaly (84.3%), is higher than the 75% mean reported by Jolly et al. (2002) at Berenty. Higher fecundity at our site may be related to the fact that group density is lower, and home range size is larger compared to Berenty (see Jolly and Pride, 1999), and therefore the number of adult females per hectare at Beza Mahafaly is lower. Such factors may translate to less intense inter-group feeding competition compared with Berenty, which could have a positive effect on fecundity.

At Berenty, 2-year-old females were found to give birth, but the rate was low, at 11.1% (Koyama et al., 2001). At Beza Mahafaly, we have noted 3-year-old, but not 2-year-old females giving birth. Again, this difference in age at first birth is likely related to better nutrition at Berenty, from both introduced fruit trees and occasional food provisioning in addi-

tion to naturally occurring food resources, and water provisioning. Koyama et al. (2001) found that fecundity increased as a function of age and was 75–85% between 5–10 years (our prime age-group). Old female fecundity was considerably reduced at Berenty. We also found that old females exhibited more variable reproductive patterns but may reproduce right up to their deaths, e.g., one 16-year-old female was observed with an associated juvenile in 2000, but she died later that year.

The fecundity pattern found in *L. catta*, i.e., very young and old adult females reproducing at far lower rates than middle- or prime-aged females, is similar to that found in several anthropoid species where fecundity has been calculated, e.g., rhesus macaques (Drickamer, 1974); toque macaques (Dittus, 1975); Japanese macaques (Koyama et al., 1992); and savannah baboons (Altmann et al., 1988).

Richard et al. (2002) argued that female white sifakas at Beza Mahafaly are "bet hedgers," i.e., they give birth later (few females successfully reproduce before age 6 years) and reproduce longer, for their body size (into their early 20s), than do other primates. Richard et al. (2002) noted that 20-year-old white sifaka females reproduce at the same rate as 7-year-olds. They suggested that this pattern is a response to an unpredictable environment. On the

other hand, the sympatric ring-tailed lemur exhibits a similar average body weight to the white sifaka (2.2 kg for ring-tailed lemurs vs. 2.8 kg for the white sifaka; Sussman, 1991; Richard et al., 2002), yet female ring-tailed lemurs reproduce early, at 2 or 3 years of age, and most continue to reproduce annually into their teens; however, females who were 13 years and over exhibited the most variation in fecundity. Thus, in contrast to the sympatric white sifaka, there may be a decline in fertility with old age in female *Lemur catta*, but more data are needed to determine if this an actual trend, as our sample size of old females is small.

In Milne-Edward's sifaka (*Propithecus diadema edwardsi*), an eastern rainforest species, females begin reproduction at 4 years of age (Wright, 1995). This species is larger than the white sifaka: average body weight is 5–6 kg (Glander et al., 1992; Wright, 1995; Pochron et al., unpublished findings), though it belongs to the same genus. It may be that female *Propithecus* begin reproduction later than *Lemur*, even if some species are of similar size to and are sympatric with *Lemur catta*. We argued elsewhere (Gould et al., 1999) that ring-tailed lemurs might be considered a "quick-recovering" or "quickly rebounding" primate species, and here we suggest that such a pattern might have evolved as a different kind of reproductive strategy, compared with sifaka, when a species must live in a highly seasonal and unpredictable environment.

Furthermore, Richard et al. (2002) suggest that white sifaka fall into the "capital breeding" category, i.e., females store resources necessary for successful reproduction, and interfemale competition is highest during the wet season, when females are neither lactating nor gestating (Stearns, 1992; Jonsson, 1997). Richard et al. (2002) also suggest that other lemur species might exhibit a similar pattern. Our long-term data on ring-tailed lemur reproduction at the same site indicate that ring-tailed lemurs at Beza Mahafaly may be "income breeders" rather than "capital breeders," i.e., females do not strongly rely upon resources such as fat stores during reproduction; rather, they use maximum resources obtained from the environment when in the process of gestation and lactation (Stearns, 1992; Jonsson, 1997). Ring-tailed lemurs lactate and wean infants during the wet season, a time of maximal food availability (Sauther et al., 1999). They also gestate during the dry season, a period of dramatic reduction in fruits, their primary food. It is unlikely that they can easily store resources for reproduction. An important implication is that ring-tailed lemurs may be more negatively affected by drought as reflected in higher infant mortality patterns, compared with sympatric white sifakas during the 1992 drought (see below).

The ring-tailed lemur is a female-philopatric species. The prediction by Wrangham (1980) that larger groups in female-bonded primate species should experience higher reproductive success due to successful foraging competition with smaller groups does not apply to the Berenty population (Jolly et al., 2002). At Beza Mahafaly, mean number of births rose with the number of females in the group, except in cases where there were 6 and 7 resident females. Thus, the prediction by Wrangham (1980) can be applied to our study population until the number of females in a group equals 5. Beyond 5, within-group feeding competition between females may be strong enough to negatively affect numbers of births. Furthermore, interfemale feeding competition is most marked during the lactation season (Sauther, 1993), and such competition may also affect the survival of unweaned infants.

Multiple births and infant mortality

Although rare, twins and even one set of triplets have been recorded at Berenty (Koyama et al., 2001; Jolly et al., 2002); however, no multiple births were observed at Beza Mahafaly over the 6 years in which data were collected in the birth season. Again, the water and food provisioning at Berenty may help explain why multiple births have been recorded there but not at our site.

At Beza Mahafaly, infant mortality in the first year of life varied from 52% in a nondrought year to 80% in a drought year. Both of these figures are considerably higher than the 37% recorded by Koyama et al. (2001) for the tourist/gallery forest areas of Berenty in a year of normal rainfall. Jolly et al. (2002) reported differential 1-year survival at Berenty, depending on where in the reserve the lemurs were residing: in the gallery forest tourist areas, where animals are occasionally food-provisioned and always water-provisioned, mean 1-year mortality was just 32.5%. In the scrub forest, similar to the forest at Beza Mahafaly, infant mortality was greater than 50%, close to what we found in a nondrought year. Clearly the introduced fruit trees, water provisioning, and occasional food provisioning at Berenty result in a dramatic decrease in infant mortality.

Interestingly, in nondrought times, *Lemur catta* infant mortality in the first year at Beza Mahafaly (52%) is very similar to that found in the sympatric white sifaka (48%), as reported by Richard et al. (2002). However, during the drought period, Richard et al. (2002) reported a lower infant mortality rate for the sifaka (66%) compared with 80% in *Lemur catta*. Possible explanations for lower infant mortality in the sifaka during this stressful period might include a slower rate of infant development in sifaka compared with ring-tailed lemurs, and maternal dietary differences which may affect milk production (primarily folivorous with a greater abundance of leaves for the sifaka vs. largely frugivorous with scarce fruit resources for the ring-tailed lemurs).

Nonetheless, in drought or nondrought years, infant mortality is high compared with mortality rates (to 1 year of age) for small to medium-sized group-living anthropoids, e.g., *Alouatta seniculus*, 16–19%

(Crockett and Rudran, 1987); *Macaca fascicularis*, 20% (van Noordwijk et al., 1993); *Cebus olivaceus*, 18.2–21.6% (O'Brien and Robinson, 1993); *Cebus capucinus*, 29% (Fedigan et al., 1996; and *Macaca maurus*, 17.1% (Okamoto et al., 2000). Factors such as low lipid and protein content in lemur milk (Tilden and Oftedal, 1997), and lower birth weights in lemurs compared to anthropoids of the same size (Rasmussen and Tan, 1992), may contribute to such overall higher infant mortality in this primate superfamily.

Life-span

Rhine et al. (2000) found that their sample population of 72 female yellow baboons took 24 years to replace itself. At Beza Mahafaly, there has been a nearly complete replacement of individuals in the 15 years since the study began. Since this is a female-bonded species, we know that collared/tagged females missing from social groups have likely died. The oldest female in the reserve population was 18 years of age in 2001, and she was exhibiting signs of advanced arthritis at this time: her head was permanently held to one side, and she climbed and leapt with difficulty. Furthermore, she was often unable to keep up with the group, and was heard repeatedly giving lost calls almost daily. Since none of the other collared females whose ages were known have survived to this age, we suggest that 18–20 years may represent the maximum life-span for naturally occurring female ring-tailed lemurs in the wild.

We know less about male life-span. Males are the dispersing sex, and some males in this population transfer to groups well outside of the reserve boundaries. Since none of the males collared in the initial 3 years of the study were present in either 2000 or 2001, and since only 3/18 males captured in 1995, the final year of collaring, were residing in the reserve in 2001, we suggest that males may have shorter life-spans than females. In a 10-year study at Berenty, Koyama et al. (in press) noted that one male in their study population lived to 13 years of age, but that no other male lived beyond 10 years.

Similarly, in the sympatric white sifaka, Richard et al. (2002) noted that males do not live as long as females. Shorter male life-expectancy and life-span in *Lemur catta* males may not make sense, considering that females are under such marked physiological stress when gestating and lactating at the height of the dry season throughout their reproductive lives. However, adult male ring-tailed lemurs experience significant costs and may die younger than females as a result of factors associated with dispersal such as greater predation risk and a lack of affiliative partners, which can lead to greater ectoparasite loads and fewer opportunities for thermoregulation over a period of several months (Sussman, 1991; Gould, 1996a,b, 1997a,b; Sauther et al., 2002). Sussman (1992) also found that dispersing males exhibited lower body weights overall than did resident males. Furthermore, while residing in a group, males must defer to females when feeding, which could lead to poor nutrition, especially during the 6–7-month dry period in this region of Madagascar. These variables considered together may result in a shorter life-span in adult males.

Group fission

Group fission appears to be a common feature in *Lemur catta* when groups reach a critical size, and fissioning has been observed at both the Berenty and Beza Mahafaly sites (Sussman, 1991; Koyama, 1991; Hood and Jolly, 1995; Jolly et al., 2002; Koyama et al., in press). At Beza Mahafaly, the first group fission occurring during the study period was in 1988 (Sussman, 1991), when Yellow Group, with 18 animals, split into two groups. Subsequently, the original group has fissioned again. These groups reside in the driest area of the reserve, furthest from the riverine-forested area. Fewer tamarind trees, the keystone resource for this species (Sauther, 1992), occur in this area (Sussman and Rakotozafy, 1994). Clearly this drier region has a reduced carrying capacity compared with the riverine area, and competition for resources is presumably high. Dittus (1998) suggested that fissioning in female-bonded primate species may occur when costs to females (intragroup resource competition) outweigh the benefits of group membership. This explanation seems to apply to the above-mentioned *Lemur catta* groups.

One difference between postfission behavior at the two sites is that at Berenty, groups that split from their original group experienced severe aggression, wounding, and socially induced infant mortality from the parent group (Hood and Jolly, 1995; Koyama, 1991), whereas at Beza Mahafaly, where group density is not as high, newly fissioned groups have not been observed participating in such extremely aggressive episodes, although agonistic intergroup encounters do occur. Such encounters involve much chasing and lunging between females and vocalizing by both females and males, but not actual attacks. Adult males, who do not play a role in resource defense in this species, have never been observed to participate in the fissioning process (Koyama, 1991; Koyama et al, in press; Hood and Jolly, 1995; personal observation).

CONCLUSIONS

We previously suggested that *Lemur catta* is a highly flexible "edge" or "weed" species (Sussman, 1977; Gould et al., 1999; Sauther et al., 1999) which has successfully adapted to highly variable habitats ranging from gallery forest, to dense brush, spiny forest, low-lying limestone forests, and even above the tree line at an elevation of 2,500 m (Goodman and Langrand, 1996). *Lemur catta* is also able to withstand extreme resource seasonality, temperature variation, and droughts (Sauther, 1992, 1998; Gould et al., 1999). Annual rainfall amounts in southwestern Madagascar are far more variable

compared to many other geographic areas inhabited by primates, and this region of Madagascar is also a high-risk area for at least one major drought every decade (Richard et al., 2002; Dewar and Wallis, 1999; Ropelewski and Halpert, 1987).

Richard et al. (2002) stress that such climatic variables have likely shaped the evolution of white sifaka life-history patterns and resulted in the "bet-hedging" reproductive strategy in females: a slowing down of female life-history and reproduction, wherein females' first births are later than expected for their size, and females also reproduce longer than expected. In the sympatric ring-tailed lemur, a somewhat different reproductive strategy has evolved in females, also related to climate and resource unpredictability in this habitat. Here, females reproduce relatively early (2–3 years of age), and many give birth annually until they die, although they are not as long-lived as the sifaka. Furthermore, there may be more variation in fecundity in old age compared with the white sifaka. We argue that such a strategy is another kind of evolutionary response to the unusual climate and environmental conditions under which this species has evolved.

ACKNOWLEDGMENTS

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