



Natural Disasters and Primate Populations: The Effects of a 2-Year Drought on a Naturally Occurring Population of Ring-Tailed Lemurs (*Lemur catta*) in Southwestern Madagascar

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We examine demographic patterns from a long-term study (1987–1996) of the population of ring-tailed lemurs in the Beza-Mahafaly Special Reserve, in southwestern Madagascar. In particular, we focus on the effects that a severe drought in 1991 and 1992 had on the population. The population of adult animals peaked in 1991 but decreased rapidly during the subsequent drought and immediate postdrought years. In the 1992 birth season (and second year of the drought) infant mortality reached 80%, and 20.8% of all adult females in the reserve died. The following year, adult female mortality reached a high of 29.9%. Juvenile mortality in 3 intensively studied groups was 57% during the second year of the drought. We compare these data with infant, juvenile, and adult female mortality in non-drought years. We are not able to calculate adult male mortality, as they often emigrate from the reserve to the adjacent forest; however, in the same 3 intensively studied groups, 89% of the males disappeared during the 2 immediate postdrought years. By 1996, the population had begun to recover after the decline that correlated with the drought conditions. Annual reproduction, high birth rates (.80–.86 annually), early sexual maturity, and dietary adaptability may be contributing factors to the recovery. Effects of and recovery from this type of natural disaster in the Beza

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Mahafaly ring-tailed lemur population parallel responses of some species of macaques and baboons with respect to the adaptability of edge species.

KEY WORDS: drought; ring-tailed lemurs; environmental effects; mortality.

INTRODUCTION

Long-term demographic studies on naturally occurring primate populations have provided us with valuable information on life-history patterns such as adult and infant mortality rates, birth rates, life spans, migration patterns, home range stability, and population variability over several years (Dunbar, 1980, 1986; Glander, 1980; Isbell, 1990; Richard *et al.*, 1991; Sussman, 1991; Strier, 1993; Wright, 1995; Fedigan and Rose, 1995; Jolly and Pride, 1999). Such information allows us a broader perspective on the interplay between primate social structure and its relation to the environment. In some cases, long-term demographic studies have revealed the effects that natural disasters such as droughts, cyclones, and fruiting failures can have on primate populations. For example, significant or marked declines in known populations as a result of environmental stress and changes in distribution or abundance of food resources occurred in vervets (Struhsaker, 1973), chacma baboons (Hamilton, 1985), toque macaques (Dittus, 1988), red colobus (Decker, 1994), and possibly 8 species of primates inhabiting the Lopé Reserve, Gabon (Tutin *et al.*, 1997). In addition to factors such as increased infant, juvenile, and adult mortality and overall population declines, periods of environmental stress resulting from such natural disasters can result in fissioning of established social groups (Dittus, 1988).

We focus on the effects that a severe 2-year drought (1991–1992) had on the population of ring-tailed lemurs (*Lemur catta*) living in the Beza-Mahafaly Reserve, in southwestern Madagascar, and compare it to demographic data collected on the population between 1987 and 1990, and again between 1994 and 1996. In particular, we consider the effects of this drought in relation to infant, juvenile, and adult female mortality, adult male group membership, and the marked decrease and subsequent recovery of the population.

RESEARCH SITE, SUBJECTS, AND METHODS

The Beza-Mahafaly Reserve, situated in southwestern Madagascar, was established as a Special Government Reserve in 1986 (Richard *et al.*, 1987). It consists of two parcels of forest: Parcel 1 is characterized by 80 ha of gallery forest, and Parcel 2 consists of 500 ha of dry adapted, desert-like *Didierea* forest (Fig. 1). Parcel 1 contains riverine vegetation, dominated

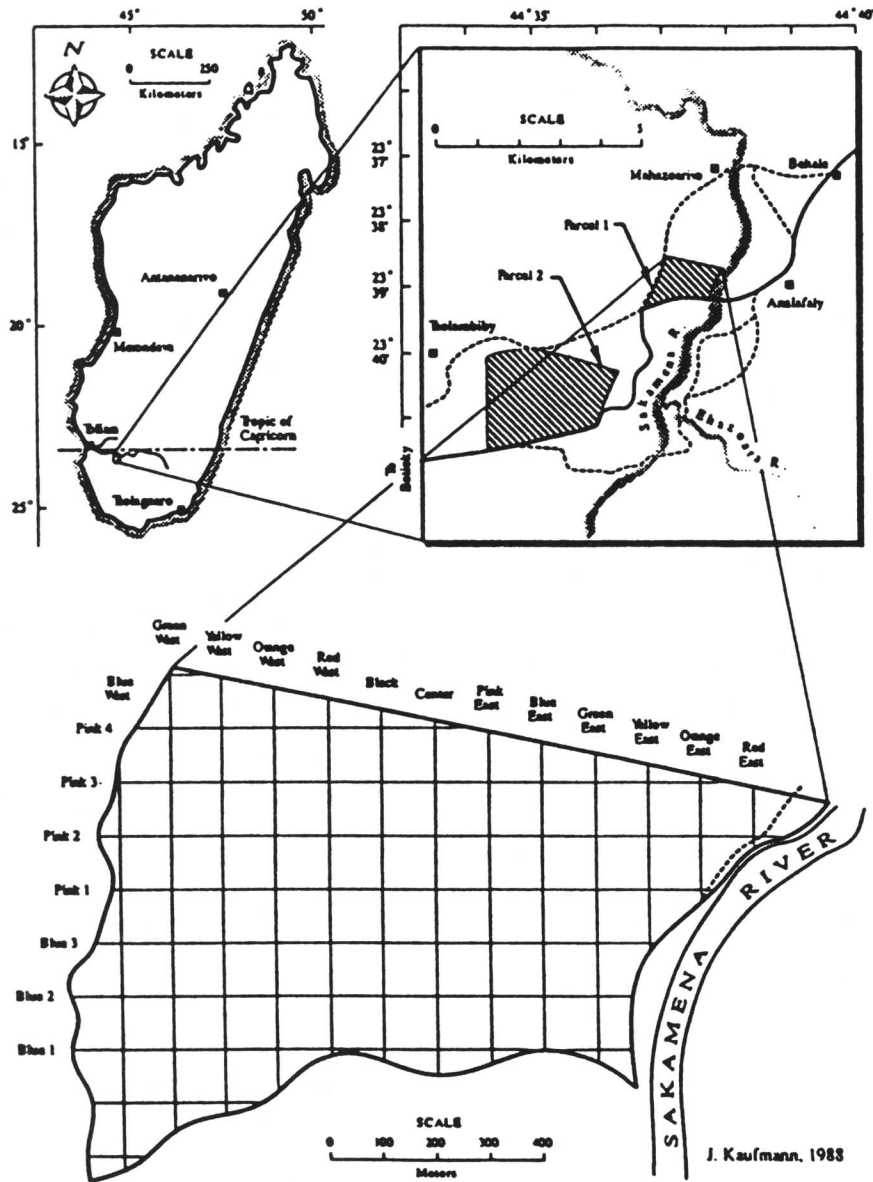


Fig. 1. Location of Beza-Mahafaly Special Reserve in southwestern Madagascar and trail map of Parcel 1.

by *Tamarindus indica* on the eastern border, and much drier forest as one moves to the western part of the parcel (Sussman and Rakotozafy, 1994).

There is marked environmental seasonality in this region (distinct hot/wet and cool/dry seasons with transitional periods between them). Food resources exploited by the lemurs are abundant during the hot/wet season and very low in both quantity and quality during the cool/wet season (Sauther, 1992, 1993). Furthermore, the Beza-Mahafaly region periodically experiences droughts. Rainfall data collected since 1945 at the Betioky weather station, 25 km southwest of the Beza-Mahafaly Reserve, indicate that droughts or marked dry seasons occurred in 1949, 1957, 1959, 1964, 1976, 1982, and 1991–1992.

Ring-tailed lemurs (*Lemur catta*) occur in riverine and xerophytic forests in southern and southwestern Madagascar (Jolly, 1966; Sussman, 1977). They live in multimale–multifemale social groups, and exhibit female residence and male dispersal (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1977, 1991, 1992; Sauther, 1991). Social groups range from 5 to 27 individuals, with a sex ratio of approximately 1:1 (Jolly, 1966, 1972; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Merti-Milhollen *et al.*, 1979; Jolly *et al.*, 1982; Sauther and Sussman, 1993).

Our demographic study focuses on the ring-tailed lemur population that resides in Parcel 1, the smaller, 80 ha area of gallery forest. The reserve boundaries join with contiguous forest throughout this region. Primates in Beza-Mahafaly Reserve include the ring-tailed lemur (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi verreauxi*), the white-footed sportive lemur (*Lepilemur leucopis*), and the gray mouse lemur (*Microcebus murinus*).

This long-term demographic project on ring-tailed lemurs began in 1987 and is described by Sussman (1991). Between 1987 and 1990 and in 1994 and 1995, we captured all adult animals residing in the 9 social groups within the reserve boundaries and fitted them with nylon collars and numbered plastic tags for identification. The collar color indicates to which group the lemur belongs, and the numbered tag identifies individual lemurs. During capture, we weighed, measured, and fingerprinted the lemurs. In most cases we made dental casts and collected hair and fecal samples. We also noted reproductive state and general physical condition.

We censused the collared groups at least once each year between 1987 and 1996, when researchers were present at the reserve (Sussman, 1991, 1992; Sauther, 1991, 1992; Gould, 1994; Nash, unpublished data; Colquhoun, unpublished data; Gould, unpublished data; Cavigelli, unpublished data). In some cases there are multiple censuses in a particular year. Because of the collaring and tagging system used, it has been possible to collect data on mortality and group transfer of known individuals, as well as documenting which subjects are involved in group fission.

The groups of ring-tailed lemurs which have been or are now present in the reserve include Red, Green, Blue (extinct), Black (extinct), Lavender

(new group as of 1995), Tan East, Tan West, Yellow, Yellow Prime, New Yellow, and Brown. Group size (adult males and females) averages 7.8 individuals and ranges from 3 to 14. In years when we could calculate group size including immatures, group size averages 11 individuals and ranges from 3 to 18 lemurs.

RESULTS

Changes in the Adult Population of Ring-Tailed Lemurs Within the Reserve

When the project began in 1987, a total of 65 adult male and female ring-tailed lemurs lived in the 9 social groups within the reserve. In early 1991 the total number of adults reached a peak of 85; however, a serious drought in the region in 1991 and 1992 affected the population, as availability of food decreased markedly. In the 2 years following the drought, the population decreased significantly ($\chi^2 = 18.09$, $df = 9$, $p < 0.05$). The total number of adult ring-tailed lemurs fell from 82 in 1992 to 70 in 1993 (a 14.6% decrease), then from 70 in 1993 to 51 in 1994 (a 27% decrease in the adult population). In the most recent census, conducted in 1996, the population appeared to be slowly recovering, with 57 adults present (Fig. 2).

Adult Female Mortality in Drought, Immediate Postdrought, and Recovery Years

Ring-tailed lemurs are highly seasonal reproducers, and in a given year, most adult females give birth (Budnitz and Dainis, 1975; Mertl-Milhollen *et al.*, 1979; Sussman, 1991; Sauther, 1992; Gould, 1994).

In a 6-month period between the end of September 1992 (drought year) and March 1993 (immediate post-drought year), adult female mortality reached 20.8% (Table I). All adult females that died then had infants and were lactating. Between 1993 and 1994 adult female mortality was even greater: 29.9%. Comparatively, in a nondrought year (1987 and 1988), adult female mortality was only 3.1%. Furthermore, between 1994 and 1995 the number of adult females in the population actually increased by 14.8%, and between 1995 and 1996 there was an increase of 12.9%. The growth in these two consecutive recovery years relates to the sexual maturity of females that were adolescent (2–3 years) when censused the previous year.

Group size, or distance of home range from the river did not appear to affect adult female mortality. Adult females died in all 9 groups during

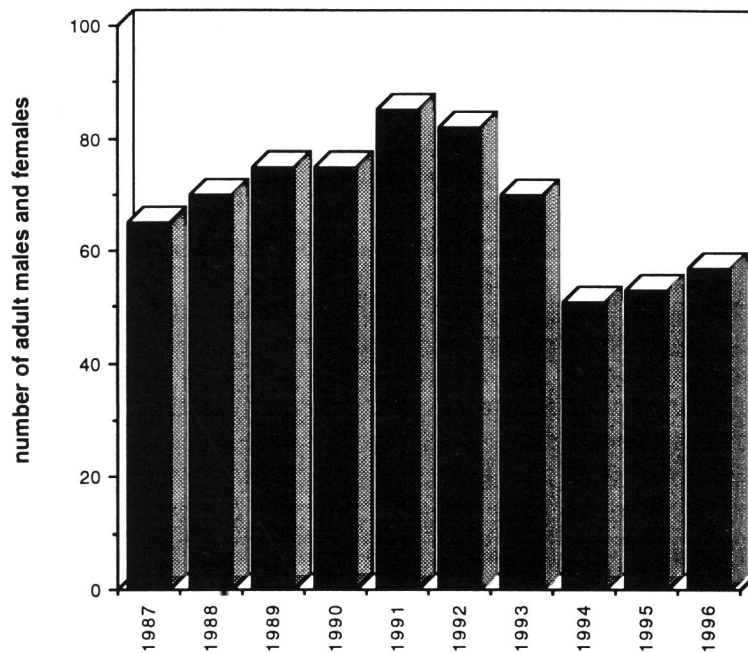


Fig. 2. Variation in the population of adult ring-tailed lemurs in the Beza-Mahafaly Reserve over a 10-year period. Whenever possible, we censused after the season of male migration (November–March). The drought occurred in 1991 and 1992.

the 2 immediate postdrought years (1993–1994), and they had home ranges that both included and did not include riverine forest and access to the river. Group size also varied, with the total number of adults ranging from 3 to 14 in the 9 groups (Table II).

Infant Mortality in Drought, Immediate Postdrought, and Recovery Years

Infant mortality was also extremely high during the drought years. Of the infants born during the 1992 (September/October) cohort, 80% had died in the 6-mo period following the birth season. Comparatively, of the infants born in the 1987 birth season, 48% died within the first year, and in the 1994 birth season, only 18% had died in the subsequent 10-mo period (Table III). Again, infant mortality did not correlate with group size or distance of home range from the river, as infants in all 9 groups died. All 9 infants in the 3 intensively studied groups died, and the home ranges of

Table I. Adult Female Mortality Comparing Drought (1992/93), Immediate Postdrought (1993/94), and Nondrought (1987/88 and 1994/95) Years

Drought years	
Number of females present in 1992	48
Number of females present in 1993	38
Adult female mortality	20.8%
Immediate postdrought years	
Number of females present in 1993	38
Number of females present in 1994	27
Adult female mortality	28.9%
Nondrought years	
Number of females present in 1987	32
Number of females present in 1988	31
Adult female mortality	3.1%
Number of females present in 1994	27
Number of females present in 1995	31
Population growth of adult females	14.8% ($n = 4$) ^a
Number of females present in 1995	31
Number of females present in 1996	35
Population growth of adult females	12.9% ($n = 4$) ^a

^aIncrease in the number of adult females between 1994/1995 and 1995/1996 relates to adolescent females in some groups reaching sexual maturity.

the 3 groups included access to the river and a large amount of riverine forest.

Juvenile Mortality

It was not possible to track juvenile mortality during the drought years as carefully as infant mortality, as juveniles cannot be collared and tagged. Therefore, for censuses conducted in 1992 and 1993 it was not possible to identify juveniles individually in all groups. With infants, it is possible to determine mortality rates, as they are either on the mother or within close proximity to the mother for 6 months. However, we documented juvenile mortality during the drought period for 3 intensively studied groups: 4 of 7 of them died. Thus, juvenile mortality in the 3 groups was 57%, lower than infant mortality during that period; infant mortality for the same 3 groups in 1992 was 100%. However, juveniles in the 3 focal groups appear to have been markedly affected by the drought, as juvenile mortality calculated in a nondrought year, 1987–1988, was only 6% (Sauther, 1992).

Table II. Age Classes^a of Females that Died in 1993/1994 (Immediate Postdrought Years), Mean Group Size in 1993/1994, Proximity of Home Range to River and Riverine Forest During Drought

Group name	Age class of females that dies in 1993 & 1994, ^a presence of infant at time of death	Mean group size (No. of adults) in 1993/1994	Home range bordered on river?
Yellow	YA, old	8	No
Yellow Prime	Old	8.5	No
Blue	Old (infant)	5	Yes
Red	OP (infant)	6	Yes
Green	Old (no infant), Old (no infant), P (infant)	8	Yes
Black	YP (Infant), P (Infant), OP (no infant)	5	Yes
Tan West	Ya (infnt), P(no infant), Old (no infant)	5	No
Tan East	YP (infant), YA (infant)	7	Yes
Brown	P, ^b Ya, ^b YA (infant), P (infant), P (no infant)	14	Yes

Total: young adults, young prime = 7; prime, old prime = 8; old females = 6

^aAge classes [from Sussman (1991)]: YA = young adult, 3–4 years; young prime = approximately 4–6 years; prime = approx. 6–9 years; old prime = approx. 9–12 years; old = over 12 years.

^bFemale died just before or during 3-week birth season; parity not known.

Adult Males

We cannot calculate adult male mortality, as males sometimes transfer out of the reserve to other groups that are extremely difficult or impossible to track. Therefore, it is not possible to comment on how the drought directly affected adult male mortality. However, in 1992 and 1993, 9 adult males residing in 3 groups within the reserve were studied extensively (Gould, 1994, 1996, 1997). By 1994, only one of them remained in the reserve.

Table III. Infant Mortality Comparing Drought (1992) and Nondrought (1987 and 1994) Years

Drought year	
Number of infants born in 1992	30
Infants surviving after 6 months	6
Infant mortality	80%
Nondrought years	
Number of infants born in 1987	25
Infants surviving after 12 months	13
Infant mortality	48%
Number of infants born in 1994	27
Infants surviving after 10 months	22
Infant mortality	22

DISCUSSION

Factors Affecting Primate Populations: Population Decline and Recovery

Predation, disease, natural disasters, decline of keystone resources, and injuries are some of the factors that contribute to mortality in naturally occurring primate populations (Struhsaker, 1973; Terborgh, 1983; Hamilton, 1985; Cheney and Wrangham, 1987; Dittus, 1988; Lovell, 1990; Janson and van Schaik, 1993; DeRousseau, 1994; Wright, 1995). In times of environmental stress, we may see the more extreme effects of these variables. If a natural disaster such as a drought or cyclone markedly affects availability of food resources, malnourished animals may not be able to withstand disease and injuries, or to protect themselves from predators, as well as animals living in a less stressful environment. For example, after a 5-mo drought in the Kuiseb River canyon, Namibia, Hamilton (1985) noted that 22 individuals in an initial population of 84 chacma baboons died or disappeared. The population decline continued for 4 years. Dittus (1988) found that the population size of toque macaques at Polonnaruwa, Sri Lanka, decreased by 15% as a result of a severe drought in the region in 1974. Another drought in 1976 and a cyclone in 1978 resulted in negative population growth in 1979 and zero growth in 1980. In a 7-year period (1964–1971), the vervet population at Masai-Amboseli Game Reserve declined by 26% as a result of a marked decrease of 3 keystone vegetation species that had provided the major food sources for the population (Struhsaker, 1973). Decker (1994) reports that over a 12-year period (1975–1987), the population of Tana River red colobus declined by 80% as a result of both a shifting river course due to flooding in the 1960s and agricultural activity in the area. By the mid-1980s, however, she noted that the population had begun to recover, due largely to a difference in feeding and ranging behaviors.

At Beza-Mahafaly, 2 years after the end of the drought period, the population of adult ring-tailed lemurs had declined by 31%. However, 4 years after the drought the population was showing signs of recovery. Such recovery may be partly explained by the annual reproduction in the species. Sussman (1991) noted that annual birth rates in the Beza-Mahafaly population average .80 to .86. Furthermore, ring-tailed lemurs are highly precocial and, in the wild, are sexually mature between 2.5 and 4 years of age (Jolly, 1966; Budnitz and Dainis, 1975; Sussman, 1991; Sauther, 1992; Gould, unpublished data). Therefore, infants born in the 1993 birth season that survived would already be considered adults by the 1996 census.

It is not unusual for edge or weed species to maintain population equilibrium, or even to expand rapidly after a marked population decline due to natural or human-induced disasters. Explosive population growth is a characteristic of macaque populations, particularly when they are associated with humans near agricultural settlements (Richard *et al.*, 1989; Lawler *et al.*, 1995). In these circumstances, macaque populations can triple within 10 years (Sade *et al.*, 1977). Lawler *et al.* 1995) noted that such rapid population growth can prevent the substantial loss of genetic variation in a population. Furthermore, they suggest that new genetic combinations that arise from rapid population expansion can enhance the adaptive response of populations in a new environment.

Both Berenstein (1986) and Decker (1994) suggest that flexibility in feeding behavior and increase in home range size are important factors that can result in recovery of primate populations. Berenstein (1986) reports that after a severe drought and fire in a Bornean rain forest, a group of long-tailed macaques successfully adapted to habitat damage by shifting to less preferred food items, such as insects, as well as charred and desiccated fruits. The group also increased its home range and engaged in more terrestrial travel.

Decker (1994) found that mature leaves made up a much higher proportion of the diet in red colobus groups between 1986 and 1988, compared with groups monitored between 1973 and 1975, and the 1986–1988 groups had increased their home range area compared to the 1973–1975 groups. She attributes the slow population recovery of Tana River red colobus to such feeding and ranging changes.

We found that some of the ring-tailed lemur groups at Beza-Mahafaly occasionally increase their home ranges temporarily, but this occurs primarily during the rainy season to correspond to the blossoming or fruiting of particular preferred food items (Sussman, 1991; Sauther, 1998; Gould, unpublished data). During the drought, the lemurs exploited food items that were of very poor quality and found within the home range boundaries, such as mature and even desiccated leaves, desiccated tamarind pods, and Mexican thistle (*Argemone mexicana*).

Group Disappearance

One of the groups that we originally captured and collared in 1987 (Blue group), which consisted of 5 adults in 1993, had disappeared by 1994. In late 1994, the two surviving females from Blue group were peripheral members of an adjacent group (Green), but were consistently targeted and chased by

the female members between September and December of 1994. By 1996 they were members of a new group that formed in 1995 (Lavender).

Infant and Juvenile Mortality

Janson and van Schaik (1993) noted that in almost every demographic study of wild primates, infant death rates are markedly higher than the rates of other age-classes, except for very old animals. Several researchers found that during periods of environmental stress, both infant and juvenile mortality rates are markedly higher than those of adults (vervets: Struhsaker, 1973; chacma baboons; Hamilton, 1985; toque macaques: Dittus, 1988). During the 1992–1993 birth and infant rearing season at Beza-Mahafaly, infant mortality reached an extreme of 80% for infants 0 and 6 mo old. The following year, after a period of resource recovery, the infant mortality rate fell to 18% for infants between 0 and 10 mo old. This is a surprising find, as Sussman (1991) noted that in an average nondrought year, infant mortality is approximately 40–50%.

Janson and van Schaik (1993) suggest that high rates of infant mortality in primate populations seem to be primarily related to predation. It also seems likely that in times of extreme environmental stress, such as severe drought, higher infant mortality may be due to malnourishment in nursing and weanling infants. Older, weaned infants and young juveniles may not be able to keep up with the group if they are weak from undernourishment, thus becoming relatively easy targets for predators. Furthermore, lemur infants tend to exhibit lower birth weights than anthropoids of the same adult size (Rasmussen and Tan, 1992), and lemur milk is low in lipids and proteins (Tilden, 1993). Wright (1995) suggested that these factors may contribute to the overall higher infant mortality in lemurs compared with anthropoid primates of similar size. Thus, ring-tailed lemur infants may be at a particular disadvantage in times of extremely low resource availability, such as drought conditions, as adult females may not be producing as much relatively lower-quality milk if they are nutritionally compromised.

Juvenile mortality was not as marked as infant mortality during the drought and immediate postdrought years; however, the relatively high mortality rate in the 3 intensively studied groups suggests that this age class was also affected by the drought conditions.

Adult Female Mortality

Hamilton (1985) found that during and after a 5-mo period of drought in Namibia, adult and subadult chacma baboon males were better able to

survive food shortages than adult females were most likely because they were able to outcompete the females. He also noted that adult females living in larger groups were better able to withstand the drought conditions than females living in smaller groups were. During the drought period at Beza-Mahafaly, adult female mortality was 20.8% and was closely related to reproductive state, as the majority of them were lactating at the time of death. Females residing in all groups within the reserve were affected. The groups varied between 6 and 18 adults. During the immediate post-drought years (1993–1994) female mortality increased to 28.9%.

In ring-tailed lemurs, females have priority of access to all resources, an evolutionary strategy likely related to the strict seasonal reproduction in this species (Jolly, 1984; Richard, 1987; Sauther *et al.*, 1998). Strong competition for food resources exists among lactating females each year following the birth season in nondrought years (Sauther, 1992, 1993), and during periods of very low resource availability, such competition would be even greater. Thus, drought conditions may result in serious malnourishment, eventually leading to death, as demonstrated by the data for drought and immediate postdrought years. Given the seasonal fluctuation of food resources at this site, lactating females are highly dependent upon the increase of resource availability that normally accompanies the onset of the rainy season (Sauther, 1998). In drought years, changes in rainfall patterns can reduce food availability, leading to dramatic mortality rates in individuals that are most vulnerable; mothers and infants. These data also suggest that there may be a strict carrying capacity in seasonal habitats such as Beza-Mahafaly. The female population was 44% larger in the drought year than in 1994, and 33% larger than in 1987, both nondrought years.

Adult Male Mortality

In 1994, 8 of 9 collared and tagged males that had been the subjects of focal animal data collection in 1992–1993 had disappeared from the reserve. It is unlikely that all of them had migrated out of the reserve in this 1.5-year period, particularly since (1) adult males migrate, on average, only every 2.5–3 years (Sussman, 1991, 1992); (2) several were high-ranking within their groups and would have accrued certain benefits compared with lower-ranking males, such as greater access to the spatially central core of the group, allowing for greater predator protection, greater opportunities for social and health-related activities such as grooming, and potentially greater access to estrous females during the mating season (Sauther, 1992; Gould, 1994, 1996, 1997); (3) abundance of food resources within the reserve boundaries is higher than outside of the reserve, where the forest

has been severely degraded due to cattle and goat grazing; and (4) there are comparatively far fewer ring-tailed lemur groups residing in the immediate area outside of the reserve than within the reserve boundaries, therefore fewer opportunities exist for males to successfully transfer to one of these groups than to a group living within the reserve boundaries.

Thus, even though we cannot track adult males once they have emigrated from the reserve, it seems likely that several of the 8 males died during the period between 1993 and 1994, perhaps as a result of physiological stress related to the severe drought conditions of 1992–1993.

CONCLUSION

The devastating effect of natural disasters on primate populations is an aspect of the discipline that field primatologists must continually anticipate. For example, forest fires in Indonesia in 1997–1998, exacerbated by a long drought related to El Niño, have destroyed vast areas of orangutan and other Indonesian primate habitat. Preliminary surveys in one large (>130,000-ha) block of logging forest in East Sumatra indicate that the area has been badly affected by a succession of fires between July and November 1997, and the species hardest-hit may be the leaf monkeys and gibbons, as large tracts of forest have been defoliated due to both drought conditions and subsequent fires (Martyr, personal communication). With respect to orangutans, although actual percentages of population declines are not yet known, there are estimates. In Bornean forests in the years leading up to the current fires, orangutan populations were as high as 20,000 to 23,000 individuals, but in the past year the population may have decreased by $\geq 30\%$ as a result of fires and drought. (The Associated Press, 1998; Rejkman via Walker, personal communication).

Wildfires in Mexico, exacerbated by droughts and record high temperatures related to El Niño, have destroyed more than 700,000 acres of forest, grassland, and farmland. Much of the destroyed forest area had previously been the habitat of populations of New World monkey species (Smithsonian Biological Conservation Newsletter, June 1988).

In 1973, Struhsaker stated that the factors controlling free-ranging primate populations were poorly understood, and few data existed at the time which suggested specifically what kinds of environmental variables regulated primate populations. Subsequently, thanks to many long-term demographic studies in the Old and New World on numerous primate species, as well as information on natural disasters and primate populations, we are now better able to understand the variable effects of the environment on naturally occurring primates.

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