A Ten-year Summary of Reproductive Parameters for Ring-tailed Lemurs at Berenty, Madagascar

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ABSTRACT. From 1989 to 1998, 204 live births were recorded for ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. Excluding unknown birth dates, the peak month of birth was September, with 82.0% (146/178) occurring during this period. The offspring sex ratio (1:1.19) was not significantly different from 1:1, and there was no association with the mother's age. The first births occurred at the ages of 2 to 4 yr. The annual birth rate was very low at the age of 2 yr (11.1%), but increased thereafter: to 50.0% at the age of 3 yr, and to 75 – 85% at the age of 4 or more years. Multiple births were very rare, since only three sets of twins and one set of triplets were recorded. As for the interbirth interval, a one-year interval was the most common (92.2%). Infant mortality within the first year was 37.7% (77/204). Neonatal mortality within the first month accounted for 31.2% of all infant deaths.

Key Words: Ring-tailed lemurs; Season of births; Age-specific fecundity; Interbirth intervals; Infant mortality.

INTRODUCTION

Recently, reproductive parameters of female primates have been analyzed by many scholars, mainly (1) to evaluate sexual selection theory (e.g. FEDIGAN et al., 1986 for Japanese macaques, *Macaca fuscata*), (2) to analyze the relationships among food supply, predation, and reproduction in wild populations (e.g. CHENEY et al., 1988 for vervet monkeys, *Cercopithecus aethiops*), and (3) to obtain basic data for colony management (e.g. RAWLINS & KESSLER, 1986a for rhesus macaques, *M. mulatta*). Thus, long-term data for many species have been reported in both free-ranging and captive conditions (e.g. ITOIGAWA et al., 1992; KOYAMA et al., 1992; WATANABE et al., 1992 for Japanese macaques; DRICKAMER, 1974; RAWLINS & KESSLER, 1986b for rhesus macaques; PAUL & THOMMEN, 1984 for Barbary macaques, *M. sylvana*).

On the other hand, there is little information available regarding wild populations of primates, except for a few species (e.g. ALTMANN et al., 1977, 1988 for yellow baboons, *Papio cynocephalus*; GOODALL, 1983, 1986 for chimpanzees, *Pan troglodytes*; TAKAHATA et al., 1998 for Japanese macaques; VAN NOORDWIJK & VAN SCHAIK, 1999 for long-tailed macaques, *M. fascicularis*).

In particular, there is very little long-term data available on reproduction in wild prosimians. For example, although many studies have been conducted on the behavior and ecology of ring-tailed lemurs (*Lemur catta*) (e.g. JOLLY, 1966; JOLLY et al., 1982, 1993; SAUTHER, 1991; HOOD & JOLLY, 1995), only two papers on the demography of free-ranging ring-tailed lemurs have been published to date (SUSSMAN, 1991; GOULD et al., 1999). We will analyze demography of free-ranging ring-tailed lemurs in a separate paper (KOYAMA et al., in prep.). RICHARD et al. (1991) reported the demography of wild sifakas (*Propithecus verreauxi*).

In the present report, we summarize ten years of data on reproductive parameters for females in a wild population of ring-tailed lemurs at the Berenty Reserve, Madagascar. In the course of our study, we have already published several papers (KOYAMA, 1991; NAKAMICHI et al., 1996, 1997; ODA, 1996; NAKAMICHI & KOYAMA, 1997). In this report, we analyze the reproductive seasonality, annual birth rate, rate of multiple births, offspring sex ratio, infant mortality, interbirth interval, and infant body weight.

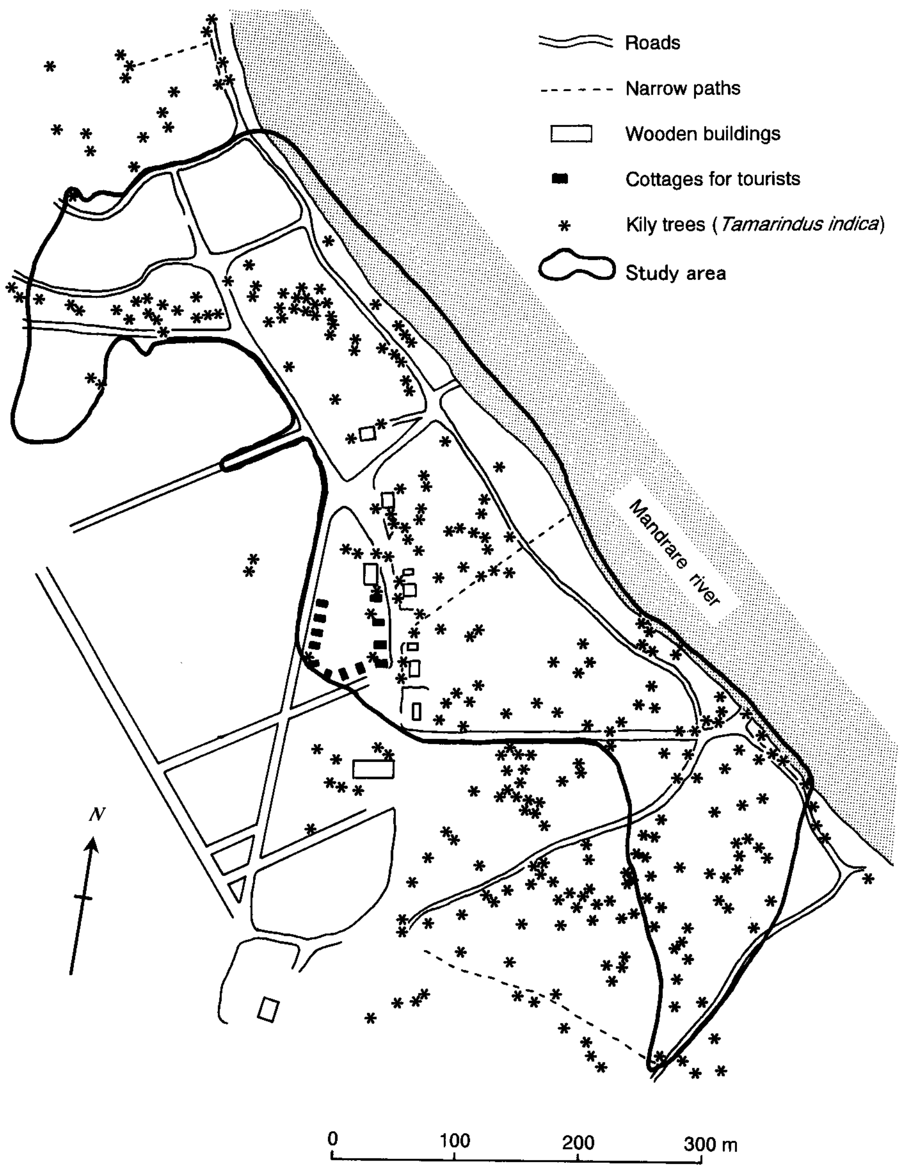

Fig. 1. The main study area and its vicinity in the Berenty Reserve, Madagascar. Note: Tourists were allowed to feed lemurs only in the neighborhood of the cottages for tourists.

STUDY AREA, SUBJECTS, AND METHODS

The main study area (about 14.2 ha, Fig. 1) was located within Berenty Reserve in southern Madagascar (KOYAMA, 1992). Annual rainfall in the study area is about 580.6 mm (mean for the period 1989 – 1998). The amount of rainfall varies from year to year; for example, annual rainfall was 911.2 mm in 1998, but only 226.0 mm in 1991. Figure 2 shows the distribution of mean monthly precipitation from 1989 to 1998. About 69.3% (402.3 mm) of the rain falls between November and February. In contrast, little rain falls during July, August, and September. There are four main types of vegetation at the reserve: canopy forest dominated by *Tamarindus indica*, open forest, brush and scrub forest, and subdesert forest, which has been cleared and replaced by a plantation of sisal, *Agave rigida* (BUDNITZ & DAINIS, 1975). Berenty Reserve consists of three forests, i.e. Malaza Forest, Ankoba Forest, and Anaramalangy Forest (see O'CONNOR, 1987). In 1998, four troops (CX, C1, C2B, and C2A) ranged within the Malaza Forest, which is dominated by *Tamarindus indica*. Two troops (T1 and T2) ranged within the Ankoba area, and about 80% of T1's range was also dominated by *Tamarindus indica*. The remaining 20% of its range and almost the entire range of T2 were dominated by introduced tree species such as *Cordia rothii* and *Pithecellobium dulce*. Three troops (C1, C2A, and C2B) range into the tourist area, and receive food supplements from tourists. Thus, the population ranges in an enriched habitat.

At the start of the study in 1989, three troops (B, C, and T) inhabited the main study area of 14.2 ha (Fig. 1). In 1989, Troop C divided into C1 and C2 (KOYAMA, 1991). By the end of August 1990, Troop B had shifted its range to a new location, about 1.3 km northwest of the former range (i.e. outside of the main study area). In 1991, Troop U2 invaded the home-range area of Troop T, and established its range within T's range. In 1993, Troop T divided into T1 and T2, and U2's range was taken over by the newly established T2. U2 retreated to an adjacent area (i.e. outside of the main study area).

In 1993, another new troop (CX) branched from Troop C1, and formed its range within the former home-range area of Troop C1. In 1997, Troop C2 divided into C2A and C2B. In 1997, HSK-Group, consisting of two adult females and one infant female, was formed by eviction from Troop T1. However, by November 1998, this group had disappeared from the study area.

The study period lasted for ten years, from September 1989 to August 1999. N. K.: September 4 – December 20, 1989; August 21 – November 22, 1990; August 19 – December 22, 1991; August 14 – September 28, 1992; August 5 – December 14, 1993; August 22 –

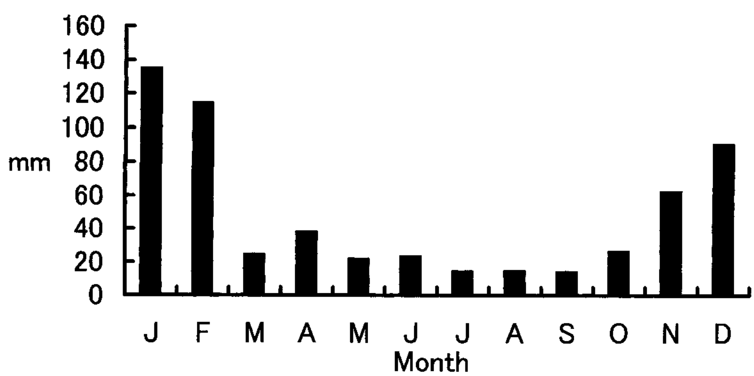

Fig. 2. Mean monthly precipitation, 1989 to 1998.

December 12, 1994; September 13 – December 8, 1995; September 10 – December 3, 1996; August 11 – September 8, 1997; August 1 – December 1, 1998. Y. T.: August 15 – October 4, 1997; August 18 – October 5, 1998. M. N.: August 22 – November 19, 1994. R. O.: August 18 – December 9, 1993; May 22 – July 3, 1994; December 24, 1994 – April 4, 1995. N. M.: August 4, 1997 – June 16, 1998. S. I.: August 1, 1998 – August 31, 1999. At the beginning of our study, the identification of individual lemurs was enhanced by spraying them with hair-dye. Subsequently, individuals have been identified using facial or other physical characteristics. Thus, all of the individuals in the study area were identified throughout the study period.

RESULTS

POPULATION GROWTH

The overall ring-tailed lemur population in the main study area increased from 63 in 1989 to 82 in 1999 (Fig. 3). Just before the birth seasons, the population density ranged between 4.4 and 7.0/ha.

The mean annual population increase was 2.7% during the study period. However, the annual growth rate varied from 25.9% in 1991 to −22.2% in 1989. Such fluctuations may have resulted from (1) inter-troop relationships (division, takeover/lose of ranges, etc.), (2) changes in the natural environment (e.g. drought), and (3) improved nutritional and water conditions.

First, the large population decrease in 1989 was mainly due to the desertion of Troop B, whose home-range was taken over by the new Troop C2 (see KOYAMA, 1991 for details). A similar troop desertion occurred in 1993, when Troop U2's range was taken over by Troop T2. Second, the population decreased again in 1993, when the birth rate was quite low and infant mortality was high (see Fig. 6). In this year, one of the staple food species (tamarind pods) also failed, which may have been due to the drought in 1991. Third, it is possible that the population increase in some troops (i.e. C1 and C2A) might have been associated with food supplied by tourists.

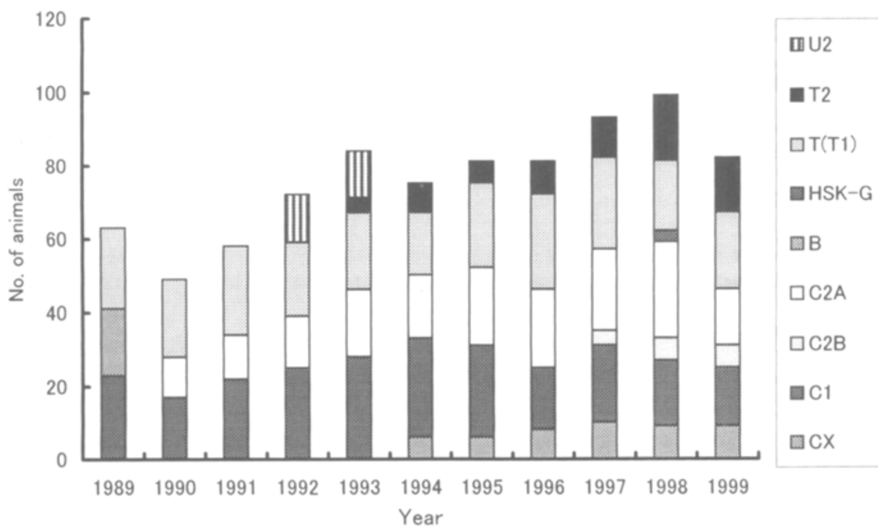

Fig. 3. Annual number of animals in each troop.

Reproductive Seasonality and Duration of Pregnancy

In 1998, N. M. observed matings of Troop C2A females, and S. I. observed their births. Thus, we obtained data on dates of estrous, duration of estrous, number of males mated, and the dates of parturition for seven individuals. In this paper, duration of estrous was defined as the length of time from the first to last mating. Based on these data, we estimated the duration of the gestation period for seven females in Troop C2A (Table 1). All of the eight adult females in Troop C2A were observed mating with males in April 1998, and we have sufficient data on the duration of estrous for four females; about 4 – 9 hr (mean=5 hr 32 min).

Excluding one adult female (*OD-90 f*), the duration of gestation ranged from 135 to 140 days (mean=138.7 days, *n*=6). After the gestation period of 177 days, *OD-90 f* gave birth to a set of twins. Her gestation was 37 days longer than those of the other six females. She might have failed to conceive on the day of mating observed in April (i.e. the first estrous cycle), and instead conceived between late May and early June (the second estrous cycle).

Births

A total of 204 infants were born in the study area (Table 2). Excluding the unknown birth dates of 26 infants, the remaining 178 births occurred between late August and late December (Fig. 4). The peak month for births was September, with 82.0% (146/178) occurring during this period. The greatest number of births occurred in mid-September. Thus, females showed strict seasonality, which coincided with austral spring and the end of the dry season.

Table 1. Name of female, date of estrous, duration of estrous, number of males mated, date of parturition, and length of gestation.

Name of female in Troop C2A	Date of estrous	Duration of estrous (hr:min)	No. of males mated	Date of parturition	Estimated duration of pregnancy (days)
OD-94 f	April 8, 1998	8:35	2	August 26, 1998	140
OD	April 15, 1998	5:45	7	September 1, 1998	139
OD-92 f	April 18, 1998	1:34+	6	September 3, 1998	138
SI	April 22, 1998	4:50+	5	September 9, 1998	140
KN	April 23, 1998	0:45+	2	September 10, 1998	140
OD-90 f	April 25, 1998	4:25	7	October 19, 1998	177*
KM	April 27, 1998	0:22	1	September 9, 1998	135

+Observations were incomplete. **OD-90 f* gave birth to a set of twins; conception may have occurred in the second estrous cycle.

Table 2. Number of births in each troop.

Year	C2A	C2B	C1	CX	T(T1)	T2	HSK-G	B	U2	Total
1989	3		5		5			7		20
1990	4		5		8					17
1991	4		8		8				1	21
1992	5		7		7				2	21
1993	4		6		4					14
1994	4		6	3	6	3				22
1995	7		6	2	6	3				24
1996	5		6	2	4	3				20
1997	4	2	4	3	5	3				21
1998	8	1	5	1	4	4	1			24
Total	48	3	58	11	57	16	1	7	3	204

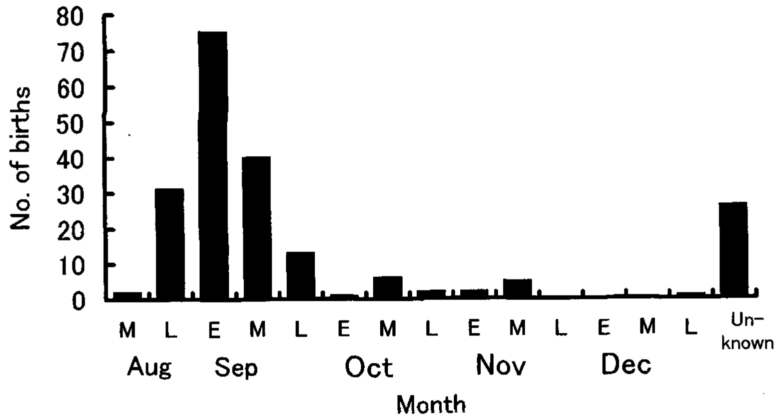

Fig. 4. Monthly distribution of births, 1989 to 1998.

The offspring sex ratio (1:1.19) was not significantly different from 1:1 (binomial test, z=1.127, p>0.2)(Table 4). There was no consistent correlation between the offspring sex ratio and the mother's age.

MULTIPLE BIRTHS

Of the 204 infants, 195 infants were singletons, six were three sets of twins, and three were one set of triplets. Four multiparous females accounted for these multiple births (Table 3). Five of these latter nine infants died within three months, and four reached adulthood. In only one case did both members of a set of twins (*MW-911 f* and *MW-912 m*) reach adulthood.

INTERBIRTH INTERVALS

The interbirth intervals were analyzed on the basis of 141 cases, involving 32 females who gave birth to 2 or more infants (Fig. 5). A one-year interval (i.e. a female had an infant from the year before) was the most common (92.2%), followed in descending order by a two-year inter-

Table 3. Multiple births.

Mother			Infant			
Name	Troop	Birth history	Name	Birth year	Sex	Notes
KYA	T	Multiparous	*KYA-901 f*	1990	Female	Died at 8 yr
			KYA-902 f	1990	Female	Died within 2 months
HIT	T	Multiparous	*HIT-901 f*	1990	Female	Alive as of August 31, 1999
			HIT-902 f	1990	Female	Died within 2 months
			HIT-903 f	1990	Female	Died within 2 months
MW	C1	Multiparous	*MW-911 f* [1)]	1991	Female	Died at 7 yr
			MW-912 m [2)]	1991	Male	Alive as of January 1999
OD-90 f	C2A	Multiparous	*OD-90981 m*	1998	Male	Died within 3 months
			OD-90982 ?	1998	Unknown	Died within 1 month

1) In 1993, this female transferred from Troop C1 to Troop CX. 2) From December 1996 to August 1997, this male transferred from Troop C1 to Troop C2. In January 1999, he left Troop C2A, and has not been observed since.

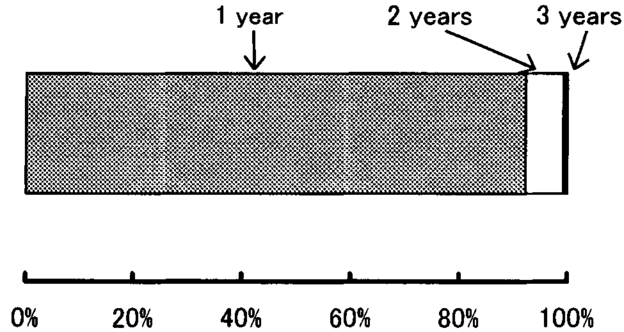

Fig. 5. Interbirth intervals.

val (7.1%) and a three-year interval (0.7%). Of the 130 cases of a one-year interval, 90 had surviving offspring from the previous year, while 40 had no surviving offspring.

Age-specific Fecundity and Overall Birth Rate

The age at which mothers gave birth was known for 24 individuals, representing 67 births (Table 4). Thirty-three females of unknown age were responsible for the remaining 137 births. The first births occurred at the age of 2 to 4 yr (m=3.2 yr, sd=0.72, n=24). Two-yr-old females accounted for only 16.7% (4/24) while most females gave birth first at the age of 3 yr (45.8% of all first births) or 4 yr (37.5%). No females gave birth to their first offspring after the age of 5.

The birth rate in 2-yr-old females was very low (11.1%, 4/36). The age-specific fecundity for females between 2 and 4 yr of age gave an ascending curve, and ranged between 75.0% and 100% for females between 5 and 9 yr of age. When we began our observations in 1989, there were 25 parous females. They were estimated to have been more than 3 yr old. Of these 25 females, 8 adult females were surviving at the end of our study, and they were at least 13 yr old. If we consider the birth rate of such females with unknown age, the birth rate may fluctuate around 75% by the age of 12 yr. Prior to their deaths, two of the females over 12 yr did not give birth to an infant for two consecutive years. Regrettably, there is still too little information available to estimate the reproductive life span of female ring-tailed lemurs.

Table 4. Age-specific fecundity, sex ratio at birth, infant mortality within the first year after birth, and mother's age.

Mother's age	No. of females	No. of births				Sex ratio (female: male)	Birth rate (%)	No. of deaths	Mortality(%)
		Females	Males	Unknown	Total				
2	36	1	2	1	4		11.1	2	50
3	26	4	7	2	13		50.0	7	53.8
4	20	8	8	1	17		85.0	5	29.4
5	14	6	6	0	12		85.7	2	16.7
6	12	5	4	0	9		75.0	1	11.1
7	8	3	4	0	7		87.5	1	14.3
8	4	1	2	1	4(*1)		75.0	2	50
9	1	1	0	0	1		100.0	0	0
Unknown	178	52	63	22	137(*4)		74.7	57	42.3
Total	299	81	96	27	204(*5)	1:1.19	66.6	77	37.7

*Nine infants were born to mothers with twins (three cases) and triplets (one case). These were each treated as a single birth to calculate the birth rates.

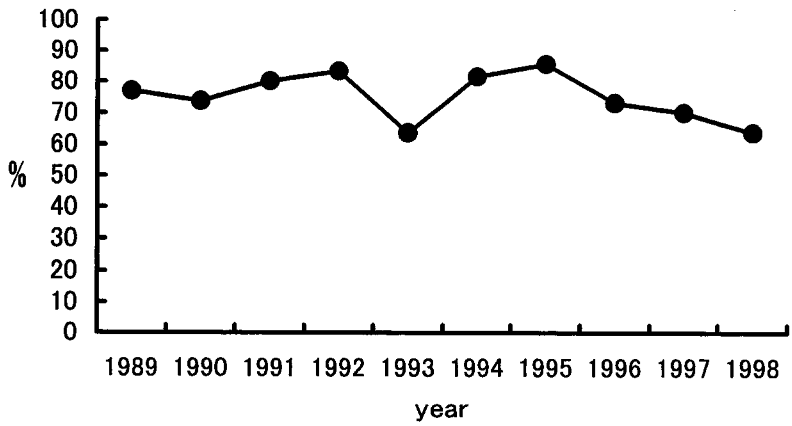

Fig. 6. Annual birth rate, 1989 to 1998.

The overall birth rate fluctuated between 63.3% (in 1993) and 85.7% (in 1995); the mean rate was 75.0% (Fig. 6). In Figure 6, 2-yr-old females were omitted from the analysis. The birth rate did not always correlate with the precipitation in the preceding rainy season. For example, the annual precipitation was only 226 mm in 1991, and the damage to crops from a drought caused an economic crisis in this area in 1992. However, the pods of the tamarind tree (*Tamarindus indica*) were rather plentiful in 1992, and the birth rate in this year reached 83.3%.

BODY WEIGHTS OF INFANTS

Body weights of seven infants were measured during capturing work conducted in early November 1998. The weight of the lightest infant at the age of 14 days was 110 g, and that of the heaviest infant at the age of 63 days was 315 g. In addition, the body weights of one dying and two dead infants were measured (Fig. 7). The weight of the dying infant at the age of 1 day was 55 g, and that of the dead infant at the age of 25 days was only 50 g. The weight of a 29-

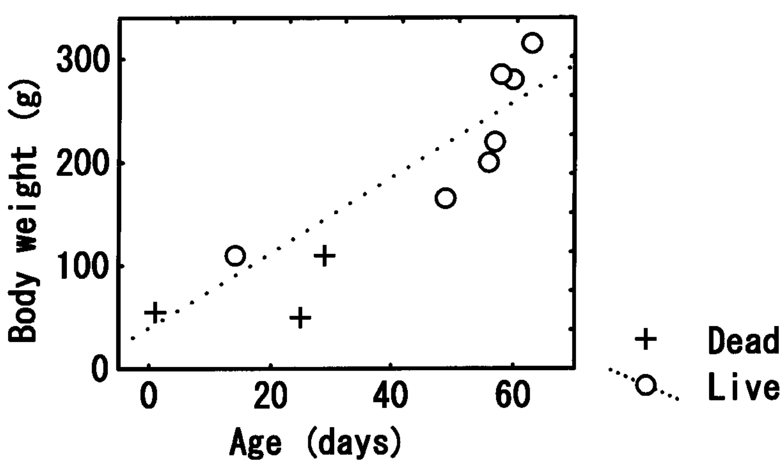

Fig. 7. Age-body weight relationships for seven living and three dying/dead infants.

day-old infant was 110 g, which is comparable to that of a healthy 14-day-old infant. It is apparent that the body weights of the two dead infants were very low for their ages. The mothers who gave birth to these infants were 3 yr old, and these were their first births.

INFANT MORTALITY

As shown in Table 4, the overall infant mortality rate within the first year after birth was 37.7% (77/204). In particular, the infant mortality rate was very high for 2-yr-old and 3-yr-old mothers. The neonatal mortality rate (within the first month) was 11.8% (24/204), and this accounted for 31.2% of all infant deaths (Table 5). The postnatal mortality (between the second and 12th months) was 26.0% (53/204), and this accounted for the remaining 68.8% (53/76) of all infant deaths.

Male infants had a slightly higher mortality rate (30.2%) than females (25.9%), however, this difference was not significant (χ^2=0.40, p>0.5). As shown in Table 5, the infant mortality rate in Troop C1 (20.7%) was significantly lower than those in the other troops (χ^2=10.03, p<0.002). This may be due to the provisioning by tourists, since Troop C1 spends much of its time around the cafeteria.

The cause of death for two of the weighed infants is known (see NAKAMICHI et al., 1996 for other accounts of infant death). The first case was observed on October 2, 1996. The body of a drowned infant (*MI-9196 f*) in Troop C2 was observed floating on the surface of the water in a drinking trough. This dead infant was 28 days old.

The second case was observed on September 14, 1998. At 08:05, Troop T2 was moving into Troop T1's range, and at 08:13 *YAK* was observed to have newborn infant with a white umbilical cord. Troop T2 passed through T1's range and went into a row of *Voandelaka* trees (*Melia azedarach*). However, members of Troop C2A had already begun eating the leaves of the trees. Most of the members of Troop T2 managed to pass through the spot, but at 08:30, when *YAK* came to this area, she was attacked by a member of Troop C2A, and her newborn infant fell to the ground, within the range of Troop C2A. *YAK* could not rescue her infant and abandoned it. At 13:45, the temperature reached 42.8°C. At 18:30, N. K. ended the observation, and collected the infant. The infant died the next morning.

Table 5. Infant mortality in each troop or group and sex.

Name of troop	No. of births	Mortality within 0 – 1 month	1 – 3 months	3 – 6 months	6 – 12 months	Total	Infant mortality within the first year (%)
C2A	48	9	4	2	8	23	47.9
C1	58	3	8	1	0	12	20.7
T(T1)	57	5	12	1	4	22	38.6
T2	16	3	3	0	1	7	43.8
CX	11	3	0	0	1	4	36.4
C2B	3	0	0	1	0	1	33.3
HSK-G*	1	0	1	0	0	1	100.0
B	7	1	5	1	0	7	100.0
U2	3	0	0	0	0	0	0.0
Total	204	24	33	6	14	77	37.7
(%)		(31.2%)	(42.9%)	(7.8%)	(18.2%)	(100.0%)	
Female	81	4	12	1	4	21	25.9
Male	96	9	10	4	6	29	30.2
Unknown	27	11	11	1	4	27	100.0

*HSK-Group was composed of two adult females and one infant.

KIDNAPPING

In 1998, N. K. observed a kidnapping among females of Troop T2. On September 19, the dominant female *SAK* gave birth to a male infant, and on September 27 – 29, her 2-yr-old daughter *SAK-96 f* gave birth to a male infant. After *SAK*'s infant died on October 22 or 23, *SAK* kidnapped her daughter's infant and adopted it. For about two weeks after the kidnapping, *SAK-96 f* took back her own infant from her mother and nursed it. However, when N. K. ceased his observation of Troop T2 on November 25, the infant was observed clinging to *SAK*. Furthermore, the actual mother *SAK-96 f* did not behave as a mother.

In addition to the 204 births recorded for the study females, another two infants were observed in the study area. We could not determine the mothers of these infants, and they were excluded from our analysis. The first case occurred on October 28, 1994. M. N. observed the adult female *MAY* of Troop T2 carrying a female infant. However, the infant died on that day and was buried. On November 8, 1994, N. K. observed *MAY* carrying a new infant (sex unknown). The infant survived up to December 9, but then disappeared from mid-December 1994 to mid-September 1995. Since the remaining two adult females (i.e. *SAK* and *YAK*) of Troop T2 had their own infants, *MAY* might have kidnapped or picked up the infant from a mother in another troop.

The second case occurred on September 20, 1998. N. K. observed an adult female *HIT-94 f* of Troop T1 carrying an infant (sex unknown). However, the infant disappeared the next day. When N. K. observed *HIT-94 f* on October 8, 1998, she carried a newborn female infant. When he observed Troop T1 on November 26, the infant was still alive. Thus, it is possible that *MAY* and *HIT-94 f* might have kidnapped these infants before they gave birth to their own infants or after they lost their own infants.

DISCUSSION

Ring-tailed lemur females are strict seasonal breeders, as pointed out by JOLLY (1966) and SUSSMAN (1991). At Berenty, births were distributed from late August to late December, but 82% of them occurred in September, which coincides with austral spring. At this study site, this birth season corresponds to the end of the dry season (see Fig. 2). According to RASMUSSEN (1985), the birth seasons of lemurs coincide with the end of dry seasons and the beginning of wet seasons, which results in lactation and weaning during times of resource abundance.

In the present study, based on the mating and birth data of six females, the duration of gestation is estimated to have been 135 – 140 days. This value agrees with the 135 days reported in the colony at the Duke University Primate Center (RASMUSSEN, 1985), the 136 days reported in the colony at the San Diego Zoo (BOGART et al., 1977), and the 136 – 145 days reported in a wild population at Beza Mahafaly (SAUTHER, 1991). Thus, at Berenty, conception must have occurred from April to mid-August. Unseasonal mating was occasionally observed (N. K., unpubl. data), and mating may result in births from October to December.

In a previous study on the mating behavior of ring-tailed lemurs, two females were receptive for about 4 hr (KOYAMA, 1988). One of the females (*PJ*) refused to allow a male to mount. In this study, the length of time from the first to the last mating was measured. In all cases, this length of time was less than 10 hr. Although the duration of estrous varies between females, it is likely that almost all females at Berenty are in estrous between 4 and 9 hr.

Only two previous reports have described female behavior at parturition among ring-tailed lemurs (SAUTHER, 1991; OKAMOTO, 1998). According to OKAMOTO (1998), the duration of parturition was 67 – 93 min for five females, and all of the mothers ate their placentas after parturition. The birth weights of ring-tailed lemurs were reported to be 50 – 70 g, and weights below 55 g were indicative of prematurity (BENIRSCHKE & MILLER, 1981). In our study, an infant that died at the age of 1 day weighed 55 g. However, its weight at parturition may have been higher, since the infant did not take milk for about 10 hr and became weakened under the hot weather conditions.

At Berenty, adult ring-tailed lemur females exhibited quite high birth rates, 75 – 85%, i.e. the birth interval was only one year for 92.2% of all births. This birth rate is as high as that reported in studies of wild ring-tailed lemurs at Beza Mahafaly, Madagascar (i.e. 86% and 80% in 1987 and 1988, respectively: SUSSMAN, 1991). At both Berenty and Beza Mahafaly, twin or triplet births were very rare or non-existent, which is quite different from the findings in the captive colony at Duke University, where 27% of births have been twins or triplets (SUSSMAN, 1991). What causes this difference? KILBORN et al. (1983) attributed the high incidence of triplet births among common marmosets to the high amount of protein in the diet of captive animals. Such nutritional conditions may affect the occurrence of multiple births among ring-tailed lemurs. RASMUSSEN (1985) reported that the lemurs with the smallest litters were from drier, more seasonal, deciduous woodlands of western Madagascar. Furthermore, while most of the 2-yr-old females at the Duke Primate Facility gave birth, very few and none of the 2-yr-old females at Berenty and Beza Mahafaly gave birth, respectively. Thus, nutritional conditions may affect reproductive parameters.

SUSSMAN (1991) reported that females at Beza Mahafaly do not give birth until their third year of age. At Berenty, some females started reproduction earlier than their conspecifics at Beza Mahafaly. The age-specific fecundity for females between 2 and 4 yr of age gave an ascending curve. The birth rate remained constant, about 75 – 85%, through the ages of 5 to 10 yr. Age-specific fecundity patterns of ring-tailed lemurs are similar to those of other primates: low fecundity in younger females followed by an increase with age and a decline at old age (DRICKAMER, 1974 for rhesus macaques; PAUL & KUESTER, 1987 for Barbary macaques; KOYAMA et al., 1992 for Japanese macaques; ALTMANN et al., 1988 for baboons, *Papio cynocephalus*). Our data may suggest that there is a post-reproductive life span for old ring-tailed lemurs, as reported for hanuman langurs, *Presbytis entellus* (SOMMER et al., 1992) and Japanese macaques (TAKAHATA et al., 1995).

The overall birth rate of the study population fluctuated from year to year, but was not directly correlated with precipitation in that year. In 1993, when the overall birth rate was quite low, the tamarind pods also failed. Unlike crops, it may have taken an extra year for tamarind fruiting to show damage from the drought. Thus, the low birth rate in 1993 may have reflected the drought in 1991. According to SUZUKI et al. (1998), birth rates among wild Japanese macaques corresponded to good or bad fruiting at the time of conception and pregnancy, and females had fewer babies after bad fruiting years than after good fruiting years.

At Berenty, infant mortality within one year after birth was 37.7%, which is much lower than the 80% recorded at Beza Mahafaly during the drought year of 1992 (χ^2=19.03, p<0.0001), but similar to the 34.6% recorded during the non-drought years of 1987 and 1994 (χ^2=0.46, p>0.4)(GOULD et al., 1999). Regrettably, most causes of infant deaths are unknown, although NAKAMICHI et al. (1996) pointed out malnutrition as a probable cause of infant death. GOULD et al. (1999) reported that at Beza Mahafaly, infant mortality was extremely high during the drought years. There may also be accidental deaths and predation by carnivores and raptors (GOODMAN et al., 1993). In the present study, one infant fell from its mother and was abandoned during an inter-troop encounter. Infanticide, the killing of unweaned young by conspecifics, was also observed once at Berenty (HOOD, 1994).

In our study area, the population of ring-tailed lemurs increased from 63 to 82 over ten years, and the average annual growth rate was 2.7%. This increase may be partly due to food provisioning by tourists and water provisioning by reserve management. The population density also increased from 4.4 individuals/ha to 5.8 individuals/ha. These values were 4 – 5 times higher than that at Beza Mahafaly (0.9 – 1.35 individuals/ha: SUSSMAN, 1991). The riverine forest dominated by tamarind trees at Berenty may have more food resources than that at Beza Mahafaly.

In the present study, kidnapping was observed among females of ring-tailed lemurs; *SAK*, the alpha female of Troop T2, kidnapped her grandson from her 2-yr-old daughter, *SAK-96 f*. Although kidnapping can be fatal when a kidnapper refuses to return an unweaned infant to its mother (NICOLSON, 1987), in this case, *SAK* took care of her grandson and successfully raised it. Since the infant mortality rate among young mothers is high (see Table 4), such kidnapping and adoption may contribute to infant survival among ring-tailed lemurs. We could not confirm whether or not *SAK* produced milk for her grandson. PEREIRA and IZARD (1989) reported that a nonpregnant, nonparous female ring-tailed lemur produced milk for unrelated infants. Kidnapping behavior was also observed in Troop A2 (BIZILY, pers. comm.). In that case, the abducting female already had her own infant, and she took care of both infants for a month, until the weaker one died. Unfortunately, it is not known whether the infant that died was her own or the one she kidnapped. In this case, the infant was kidnapped from a rival from a different matriline. Following the death of the infant, the kidnapper attempted to pull a surviving infant from another female of the rival matriline. Despite repeated attempts over two days, the mother resisted and raised her own infant.

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