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Population and Social Dynamics Changes in Ring-tailed Lemur Troops at Berenty, Madagascar Between 1989 – 1999

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ABSTRACT. In the present study, we recorded all births, immigrations, deaths, and emigrations for a population of ring-tailed lemurs at Berenty Reserve, Madagascar, between September 1989 and August 1999. In September 1989, three troops (C, B, and T) inhabited the study area of 14.2 ha. During the 10-year period, eight troop divisions, six evictions of females, and three troop takeovers of ranges by other troops occurred in and around the study area. Consequently, in August 1999, the number of troops in the same area increased to six (CX, C1, C2A, C2B, T1, and T2). The number of lemurs aged >1 year increased from 63 to 82, which resulted from 204 births, 58 immigrations, 125 deaths, and 118 emigrations. Of the 204 newborn lemurs during the study period, 103 died, 44 emigrated outside the study area, and 57 remained within the study area. The total number of lemurs that emigrated from natal troops was 69 (54 males and 15 females). Natal males left their troops around the age of 3. Non-natal males changed troops after a tenure varying from 1 to 7 years. Survival curves showed a fall in survival rates of both sexes to < 0.5 between the ages of 2 and 3. For females, the survival rate gradually decreased to < 0.2 at the age of 9. On the other hand, due to emigration, the survival rate of males could not be determined after the age of 5 yr. Since some males attained high-rank at the age of 6 – 10 yr, the prime age for male ring-tailed lemurs is thought to be around 7 – 10 yr. Ring-tailed lemurs are essentially female philopatric, because all cases of females leaving natal troops resulted from troop divisions or forced evictions. Such social changes may have resulted from competition among females. All cases of troop divisions or evictions occurred in larger troops consisting of ≥20 lemurs, and only a few females could rejoin their troops. When males joined such a female-group, a new troop was formed. Although promoted by an increase in population, frequent emigrations of females from original troops are the characteristics of ring-tailed lemurs at Berenty.

Key Words: Ring-tailed lemurs; Demography; Age of emigration; Survivorship curve; Madagascar.

INTRODUCTION

Population dynamics is a very important theme involving the understanding of life history and social structure of the species concerned (for review see DUNBAR, 1986). Many studies on simians have been published (DITTUS, 1975; ALTMANN et al., 1985; RAWLINS & KESSLER, 1986; OKAMOTO et al., 2000; SAMUELS & ALTMANN, 1991; GOODALL, 1983, 1986). However, only a few have analyzed the population dynamics of prosimian species (SUSSMAN, 1991; RICHARD et al., 1991; WRIGHT, 1995; JOLLY et al., 2002). To our knowledge, only two reports investigated the male migration of ring-tailed lemurs (SUSSMAN, 1992; JONES, 1983), but both studies were short-term. Another study examined the life history of the red-fronted lemur (OVERDORFF et al., 1999). The paucity of information may largely be due to the lack of long-term studies on prosimian populations.

JOLLY et al. (2002) analyzed the demography of ring-tailed lemurs inhabiting 1 km^2 area of Berenty Reserve, Southern Madagascar. They reported that the non-infant population fluctuated from 100 to 280 during the study period of 1972 to 1997, and the number of troops increased from 12 to 24. They concluded that (1) troop structure has a direct effect on population growth; larger troops have a lower birth rate; (2) reproductive success varies from year to year, and the drought years were associated with low birth rate and 1-year survival, and years of heavy rains after drought were even worse; and (3) it is still an open question whether the artificially high population by tourist food supplementation is dangerous for the forest.

In this report, we present more detailed analysis of a population of ring-tailed lemurs inhabiting the richest areas in the gallery forest of the Berenty Reserve, Southern Madagascar, based on long-term observation with individual identification. Specifically, we focused on, (1) 10-year changes in the population; (2) 10-year changes of troops (e.g. troop division, eviction from troops, new troop formation); and (3) male and female life-histories, with special references to immigration, death, and emigration. Please see our recent study (KOYAMA et al., 2001) for details on birth rates. We report in the present study on the population changes and male and female life histories, and discuss whether females are philopatric or not.

STUDY AREA, SUBJECTS, AND METHODS

The population of ring-tailed lemurs of Berenty Reserve in Southern Madagascar has been studied by JOLLY and her colleagues since the 1960s (JOLLY, 1966; JOLLY et al., 1982, 1993; JOLLY & PRIDE, 1999; HOOD, 1994; HOOD & JOLLY, 1995). In this reserve, the annual rainfall is about 580.6 mm (mean for the period 1989 – 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.

JOLLY et al. (2002) analyzed the demography of ring-tailed lemurs inhabiting 1 km^2 area of this reserve. They classified the vegetation of Berenty Reserve into several types/areas: (1) Ankoba: largely regrown forest with non-native trees from cleared ground; (2) Tourist Front (part of the western boundary of the Reserve, studded with tourist bungalows); (3) Gallery Forest (natural forest, with canopy covering more than 50% of the sky); and (4) Scrub forest (drier natural forest with more than 50% open sky).

Our main study area (about 14.2 ha) was located in the center of this Reserve (KOYAMA et al., 2001), corresponding to the "Tourist Front" and "Gallery Forest" in Figure 1 of JOLLY et al. (2002). This area is a mosaic of rich gallery forest dominated by *Tamarindus indica*, secondarily enriched forest dominated by *Cordia rothii* and *Pithecellobium dulce*, and the tourist area where tourists often fed bananas to lemurs from 1985 – 1999. Banana feeding has nearly stopped since 1999, with large panels warning visitors against feeding lemurs.

A preliminary study was conducted by the principle author (NK) during the period from October 2 – October 18, 1988, in which a population of ring-tailed lemurs were individually identified and studied (KOYAMA, 1988, 1991, 1992). The present study spanned over ten years, from September 1989 to August 1999. It included several trips to the Reserve by the team members (NK: 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 – December 12, 1994; September 13 – December 8, 1995; September 10 – December 3, 1996; August 11 – September 8, 1997; August 1 – December 1, 1998; YT: August 15 – October 4, 1997; August 18 – October 5, 1998; MN: August 22 – November 19, 1994; SI: August 1, 1998 – August 31, 1999).

Initially, we sprayed individual lemurs with a hair-dye for easy identification. Subsequently, the lemurs were identified using facial or other physical characteristics. In 1989, there were 63 lemurs belonging to three troops (C, B, and T) (see Fig. 1 & Table 1). Then, all of the lemurs in the study area were identified throughout the study period (NAKAMICHI & KOYAMA, 1997; NAKAMICHI et al., 1996, 1997). The population which JOLLY et al. (2002) studied included four of the same troops (i.e. C1, C2A, C2B, and CX) as this population.

During the study period, "eviction of females" and "troop division" occasionally occurred, and most of such cases may have originated from female competition over local resources. One or several females became the target of persistent aggression by other females, and they were eventually evicted from other troop members. Such a case is called the "eviction of females" (see also VICK & PEREIRA, 1989). The evicted females were rarely able to rejoin their original troops, and in several cases, they could not establish a stable home range and disappeared from the study area. On the other hand, some evicted females occasionally established a new home range, and mature males joined them, forming a new reproductive social unit (i.e. troop). Such a case is called "troop division." In other cases, evicted females sporadically fought with females belonging to another troop, and they dominated over the females. Then, the two female groups eventually melted into one troop. Such a case is called "troop fusion." Other evicted females joined other troops without aggressive fighting, which is called "female transfer."

STATISTICAL ANALYSIS

All data were expressed as mean ± SD. Differences between groups were examined for statistical significance using the Student's *t*-test. Correlations between variables were examined by Pearson regression analysis. A p value less than 0.05 denoted the presence of a statistically significant difference.

RESULTS

OUTLINE OF POPULATION CHANGES

From 1989 to 1999, the population of the study area increased from 63 lemurs to 82 lemurs (4.4 individuals/ha to 5.8 individuals/ha) [(a) and (b) in Table 1]. The mean rate of increase was

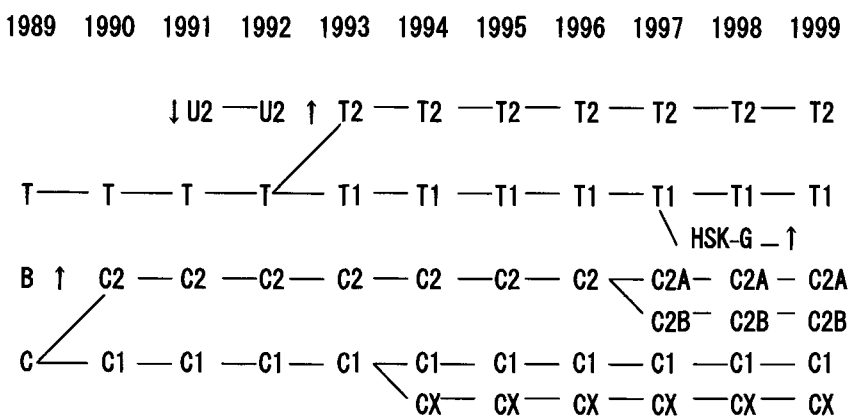

Fig. 1. A schematic explanation of troop divisions. ↓ : Immigration to the main study area; ↑ : disappearance from the main study area.

Table 1. Annual increase in the number of ring-tailed lemur population.

			Size of each troop										Number of lemurs of each age/sex class										
Year	(a)	(b)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	Mean	AF	AM	SAF	SAM	JF	JM	JU	(c)	(d)	(e)	(f)
1989	63	4.4	–	–	23	–	22	–	–	18	–	21.0	26	16	3	4	5	6	3	1:0.615	0.333	49	−22.2
1990	49	3.5	11	–	17	–	21	–	–	–	–	16.3	19	16	1	5	4	4	0	1:0.842	0.286	58	+18.4
1991	58	4.1	12	–	22	–	24	–	–	–	–	19.3	20	21	2	5	6	5	0	1:1.05	0.310	73	+25.9
1992	73	5.1	14	–	26	–	20	–	–	–	13	18.3	25	21	6	7	7	7	0	1:0.84	0.370	84	+15.1
1993	84	5.9	18	–	28	–	21	4	–	–	13	16.8	28	30	6	7	7	6	7	1:1.07	0.393	75	−10.7
1994	75	5.3	17	–	27	6	17	8	–	–	–	15.0	27	33	3	6	6	2	4	1:1.22	0.280	81	+8.0
1995	81	5.7	21	–	25	6	20	6	–	–	–	16.2	28	34	2	4	5	8	0	1:1.21	0.234	81	0.0
1996	81	5.7	21	–	17	8	26	9	–	–	–	16.2	27	25	4	7	6	12	0	1:0.96	0.358	93	+14.8
1997	93	6.5	22	4	21	10	25	11	–	–	–	15.5	31	30	6	12	7	7	0	1:0.97	0.344	99	+7.5
1998	100	7.0	26	6	19	9	19	18	3	–	–	16.2*	35	35	4	6	12	8	0	1:1	0.300	82	−18.0
1999	82	5.8	15	6	16	9	21	15	–	–	–	13.7	30	26	7	8	6	5	0	1:0.87	0.317		
Mean												16.1								1:0.968	0.320		+2.7

(a) Number of lemurs at the beginning of September in each year (New born infants born in August were excluded); (b) population density per ha; (c) adult sex ratio (adult female: adult male); (d) proportion of immature individuals; (e) number of lemurs at the next August; (f) population changes (%). (1) C2/C2A; (2) C2B; (3) C/C1; (4) CX; (5) T/T1; (6) T2; (7) HSK-group; (8) B; (9) U2 troops. AF: Adult female; AM: adult male; SAF: sub-adult female; SAM: sub-adult male; JF: juvenile female; JM: juvenile male; JU: juvenile sex unknown. *HSK-G was excluded from the calculation.

2.7% per year, although there was a great variation from −22.2% to 25.9% throughout the 10-year period [(f) in Table 1]. This increase resulted from 204 births, 58 immigrations, 125 deaths, and 118 emigrations (Table 2).

Adult individuals formed about two thirds of the whole population. In 1989, the proportion of immature individuals was 0.333 [(d) in Table 1], which scarcely fluctuated during the study period, and without consistent correlation with time ($r=-0.036$, $p>0.9$) or population density ($r=0.255$, $p>0.4$).

During the study period, the adult sex ratio (adult females vs adult males) fluctuated from 1:0.615 to 1:1.22, but without consistent correlation with time ($r=0.291$, $p>0.3$), population density ($r=0.309$, $p>0.3$), or mean size of the troop ($r=0.382$, $p>0.2$) [(c) in Table 1]. Pooled data showed that the mean number of adult males per adult female was 0.968.

The number of troops increased from three (Troops C, B, and T) to six (Troops C1, CX, C2A, C2B, T1, and T2) during the study period (Fig. 1). Pooled data showed that the mean troop size was 16.1 (SD=7.0). Although, the mean troop size/year decreased significantly with time ($r=0.809$, $p<0.03$) (Table 1), there was no significant correlation between troop size and population density ($r=-0.4895$, $p>0.1$).

Births

A total of 204 births occurred during the study period (Table 2) (for details, see KOYAMA et al., 2001). Of these, 103 died, 44 emigrated from the study area, and 57 lemurs were still within the study area at the end of study. Of the latter group, 25 left their natal troops and immigrated to other troops within the study area.

Immigration to the Study Area

Among the total number of immigrants ($n=58$), 91.4% ($n=53$) were adults (Table 2). In addition, four juveniles, and one infant ($n=5$) immigrated to the study area. Most of the latter group immigrated with their mothers, as the result of takeovers of ranges by invading troops.

Males accounted for 77.6% ($n=45$) of the total immigrants, and females for 22.4%. Out of those, 12 lemurs (7 females and 5 males) belonging to Troop U2 immigrated *en masse* to the study area (see below). In 1998, two adult females (*KM* and *KN*) immigrated to Troop C2A from outside of the study area.

Deaths

During the study period, 125 lemurs died (Table 2). Infant deaths accounted for 61.6% of all deaths. Excluding 30 lemurs of unknown sex (27 infants and 3 juveniles), female deaths accounted for 60.0% and male 40.0%. Thus, the number of deaths for males was smaller than that of females, but this may be because some of the males who were included in "emigration" would have already died.

Emigration from the Study Area

Out of the 118 lemurs that emigrated from this population, 90 (76.3%) were males, and 28 (23.7%) were females. Adult males alone accounted for 56.8% (67/118) of all emigrations from the population. Thirty-three lemurs (24 females and 9 males) belonging to Troop B, Troop U2, and HSK-Group emigrated *en masse* from the study area (see Fig. 1). Excluding these cases, males accounted for 95.3% (81/85) and females 4.7% (4/85).

Table 2. Number of birth, immigration, death, and emigration of study population.

	Year											Lemurs born during the study				Lemurs with unknown birth records			
	1989 -1990	1990 -1991	1991 -1992	1992 -1993	1993 -1994	1994 -1995	1995 -1996	1996 -1997	1997 -1998	1998 -1999	Total	Female	Male	?	Total	Female	Male	?	Total
Birth	20	17	21	21	14	22	24	20	21	24	204	81	96	27	204	–	–	–	–
Immigration into the study population	6	8	14	7	5	6	1	1	5	5	58	0	0	0	0	13	45	0	58
Sub-total	26	25	35	28	19	28	25	21	26	29	262	81	96	27	204	13	45	0	58
Death	17	8	11	12	13	12	11	7	9	25	125	42	34	27	103	16	3	3	22
Emigration from the study population	23	8	9	2	19	9	8	8	9	23	118	6	38	0	44	22	52	0	74
Sub-total	40	16	20	14	32	21	19	15	18	48	243	48	72	27	147	38	55	3	96
Total	–14	9	15	14	–13	7	6	6	8	–19									

The total number of emigrants from the study area of known age was 44 (Table 2). In addition, 25 lemurs born in the study area left their natal troops and immigrated into some non-natal troops of the study area, and still belonged to the study population. With regard to the lemurs with unknown birth records, 58 immigrated, 22 died, and 74 emigrated from the study population.

Table 2 shows that 77.9% of the increase in population was caused by new births and 22.1% by immigration. On the other hand, 51.4% of the decrease in population was caused by emigration and 48.6% by death.

Figure 2 shows the composition of the population on September 1, 1999. Out of the 82 lemurs (43 females and 39 males), the ages of all juveniles, all sub-adults, and 32 adults were known, while the exact ages of 24 adults (9 females and 15 males) were not known. However, it was possible to estimate the approximate ages of seven adult females that had reached adulthood at the beginning of the study in 1989. Table 3 shows such estimates for the ages of 24 adults.

Outlines of Troop Divisions and Evictions from the Troop

Outlines of Troop Divisions and Evictions

In 1988, when the principle author (NK) conducted a preliminary survey, there were three troops (T, B, and C) in the study area of 14.2 ha. During the 10-year study period, three troop divisions and five evictions occurred within the study area (Fig. 1 & Table 4). Out of five cases of evictions, two resulted in troop fusion (i.e. the formation of Troop CX; see the following for the details). In another case, the HSK-Group emigrated from the study area. One adult female (*KI*) could rejoin her troop. Furthermore, two adult females (*KM* and *KN*) and one infant (*KN-98*♀) could rejoin their troop.

Division of Troop C and take over of Troop B range by Troop C2: In 1989, Troop C divided into

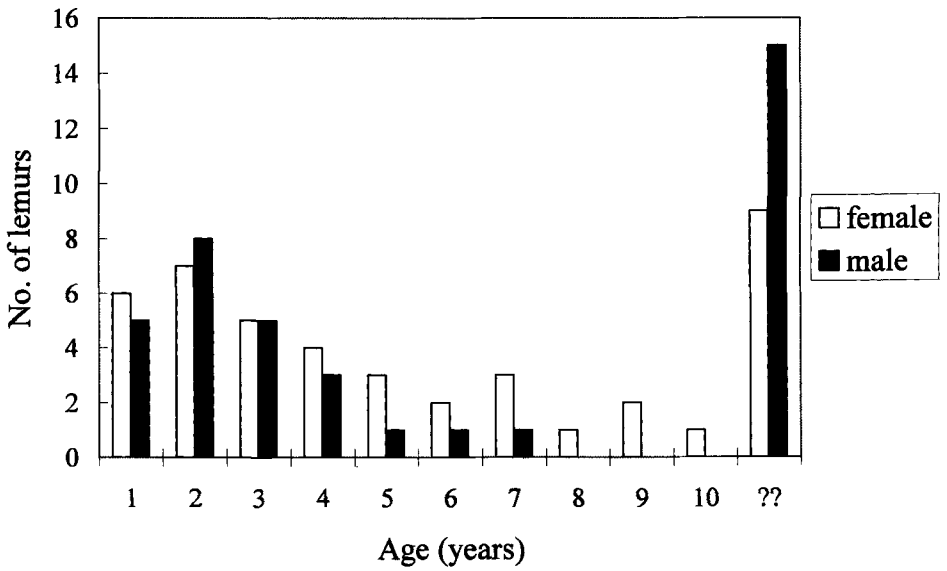

Fig. 2. Age-sex composition in the study area on September 1, 1999.

Table 3. Estimates of ages of 24 adult lemurs.

Troop	Name	Sex	Estimated age on September 1, 1999 (years)	Alive or dead (by the end of November 2000)
C2A	*OD*	f	13+	Alive
C2A	*SI*	f	13+	Alive
C2A	*KM*	f	5+	Alive
C2A	*KN*	f	5+	Alive
C2B	*RH*	f	13+	Alive
C2B	*MI*	f	13+	Alive
T1	*HIT*	f	13+	Dead by August 2000
T2	*YAK*	f	13+	Dead by August 2000
T2	*SAK*	f	13+	Alive
C2A	*OT*	m	12*	Dead on October 2000
C2B	*TJ*	m	11 – 12	Alive
C2A	*DB*	m	9+	Disappeared by August 2000
C2A	*DEK*	m	7+	Alive
C2A	*LN*	m	4+	Alive, Transferred to Troop T1
C1	*STO*	m	4+	Disappeared by August 2000
C1	*WKO*	m	4+	Alive
C1	*KUR*	m	8+	Disappeared by August 2000
C1	*HTO*	m	3+	Alive
C1	*AKM*	m	3+	Disappeared on September 2000
T1	*NME*	m	9+	Alive
T1	*INT*	m	7+	Alive, Transferred to Troop T1B
T2	*HMS*	m	9+	Alive
T2	*KIT*	m	9+	Alive
T2	*SPO*	m	9+	Alive

13+: The estimated age is more than 13 yr old; * This male was born in 1987. He left Troop A and transferred into Troop C1 during the period from 1990 – 1991. He left Troop C1 and transferred into Troop C2.

Troop C1 and C2, resulting in an increase in the number of troops from three to four (for details, see KOYAMA, 1991). However, by early August 1990, Troop C2 took over the whole range area of Troop B, and the number of troops decreased from four to three.

Division of Troop U and invasion of Troop U2 into Troop T range: By 1990, Troop U had a home range adjacent to Troop T and its range was located outside of the study area. On October 10, 1991, Troop U consisted of 25 lemurs including 3 newborn infants. On November 4, nine animals including one newborn infant (Troop U2) were observed to move independently from other members (Troop U1). Then, Troop U2 invaded Troop T range. They eventually established their range by taking about 35% of former T range. Troop U2 range was almost identical to Troop T2 range shown in Figure 4. As a result, there were four troops within the main study area.

Division of Troop T and take over of Troop U2 range by Troop T2: On August 18, 1993, Troop T was composed of 24 lemurs. On September 6, 1993, three adult females (*YAK, SAK*, and *MAY*) and one adult male (*JOU*) separated from the main troop (Troop T1), forming a new troop (Troop T2). Troop T2 invaded Troop U2 range, which originally belonged to the former Troop T range. After severe fighting with the members of Troop U2, Troop T2 took over U2 range. Consequently, Troop U2 emigrated from the study area and established its range adjacent to Troop T2.

Table 4. Social changes occurred in and around the study area during 1989 to 1998.

Year	Original troop	Daughter troop	Evicted females	Consequences
Within the study area				
1989	C	C1 and C2		Troop C2 took over Troop B's range.
1993	T	T1 and T2		Troop T2 took over the Troop U2's range, but shared former T's home range.
1993	C1		1 AF, 1 SAF	Led to the formation of Troop CX.
1995	C1		3 AF (SH-group)	SH-group dominated over females of Troop CX, and melted into one (troop fusion).
1996	C2		1 AF (*KI*)	*KI* returned to Troop C2A.
1997	C2	C2A and C2B		Troop C2B established small home range between Troop C2A's and C1's ranges.
1997	T1		2 AF, 1 IF	Led to the formation of HSK-group, who eventually disappeared from the study area.
1998	C2A		2 AF, 1 IF	*KM*, *KN*, and *KN-98* ♀returned to Troop C2A.
Around the study area				
1990	B		4 AF (SN-group)	SN-group dominated females of Troop W, and melted into one (troop fusion).
1991	U	U1 and U2		Troop U2 took over a part of Troop T's range.
1992	A	A1 and A2		Troops A1 and A2 shared former home range.
1993	D	D1 and D2		Troop D2 shifted to the southern area, but occasionally invaded into C1's and CX's ranges.
1994	E	E1 and E2		Troop E2 shifted to the southern area, but occasionally invaded into E1's range.
1996	W	W1 and W2		Troop W2 established small home range between Troop W1's and V's ranges.

AF: Adult female; SAF: subadult female; IF: infant female.

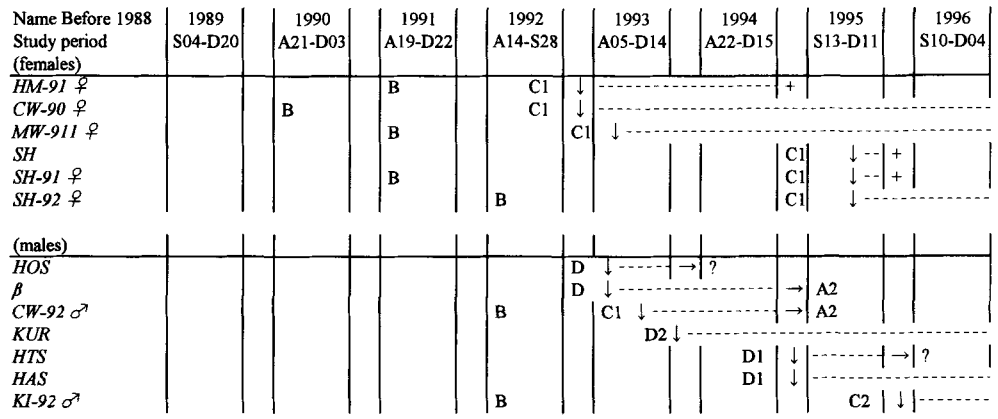

Fig. 3. A diagram explaining the changes in membership of Troop CX. Only main members were listed. -------: The period of surviving in Troop CX; ↓ : immigration; →: emigration or disappearance; + : death; B: the year of birth.

Formation of Troop CX: The process of formation of Troop CX was a little bit different from other cases. During the period from 1991 to 1992, an adult female (*HM*) of Troop C1 disappeared. Moreover, another adult female (*CW*) of Troop C1 disappeared during the period from 1992 to August 1993. We believe that these two adult females probably died. Then, their two orphaned daughters (*HM-91* ♀ and *CW-90* ♀) stopped moving with other troop members.

In 1993, Troop D, which had a home range adjacent to Troop C1 and its range was outside of the study area, divided into Troop D1 and Troop D2. Thereafter, two adult males (*HOS* and *β*) from Troop D joined the 2-female-group, and a new Troop CX was formed in the southern part of the former range of Troop C1 (Figs. 3 & 4). As a result, the former Troop C1 ranges were shared between Troop C1 and Troop CX. In October 1993, one sub-adult female (*MW-911* ♀) and one juvenile male (*CW-92* ♂) joined Troop CX from Troop C1. During the period from 1993 to 1994, the dominant male (*HOS*) disappeared and a new adult male (*KUR*) from Troop D2 joined Troop CX. During the period from 1994 to 1995, the dominant female (*HM-91* ♀) and her infant (*HM-9194* ♀) disappeared (they probably died), and two males (*β* and *CW-92* ♂) left Troop CX and transferred into Troop A2. Instead, two adult males (*HTS* and *HAS*) joined from Troop D1. In the middle of September 1995, three adult females, *SH* (mother), *SH-91* ♀, and *SH-92* ♀(her daughters), were evicted from Troop C1, and they (SH-Group) moved into the home range area of Troop CX. For about one month, severe fighting erupted between females of Troop CX and the three females belonging to the SH-Group. Eventually, the SH-Group dominated over the females of Troop CX, and they melted into one (Troop CX). During the period from 1995 to 1996, two adult females (*SH* and *SH-91* ♀) and one adult male (*HTS*) disappeared. Furthermore, an adult male (*KI-92* ♂) from Troop C2 joined Troop CX.

Eviction and return of a female from Troop C2 and formation of Troop C2B: On September 10, 1996, we noticed one adult female (*KI*) was missing from Troop C2. She was observed roaming around the peripheral area of Troop C2, within the home range area of Troop C1. She must have been evicted by the dominant females (i.e. *RH, MI,* and *MI-91* ♀) of Troop C2.

At the end of November 1996, the eight adult females of Troop C2 were ranked in this order: *RH, MI, MI-91* ♀, *OD, SI, OD-90* ♀, *OD-92* ♀, and *OD-94* ♀. Then, Troop C2 divided into Troop C2A and Troop C2B by August 17, 1997. Troop C2B was composed of three adult

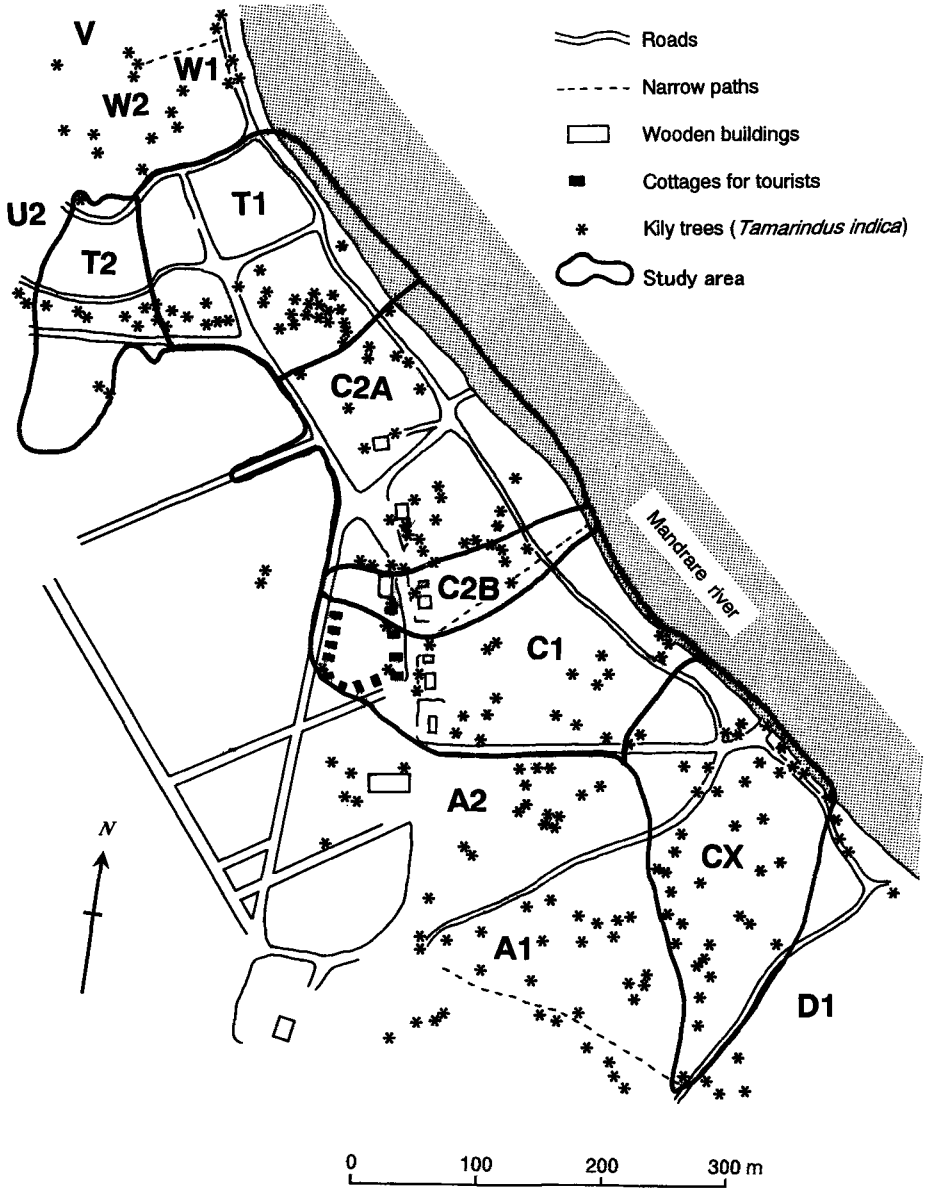

Fig. 4. Home ranges of six troops and approximate location of the neighboring troops in 1999.

females (*RH, MI,* and *MI-91* ♀) and an adult male (*NT*). In the previous year, *NT* was the third-ranking adult male of Troop C2. We have no data about the process of troop division, but it is likely that dominance rank reversal had occurred between the top three adult females and the other five adult females, and the formers were evicted from Troop C2. On the same day, 1997, we found *KI* moving together with the members of Troop C2A. We do not know when she returned to the troop, either before or after the troop division, or whether she contributed to the eviction of the RH-Group or not.

Eviction by members of Troop T1 and formation of HSK-Group: On August 31, 1997, Troop T1 was composed of 26 individuals. In late September 1997, two adult females, *HSK* (mother) and *HSK-94* ♀ (her daughter), and one infant (*HSK-97* ♀) were evicted by members of Troop T1. The HSK-Group could not establish their own range, and in November 1998 they disappeared from the study area.

Eviction and return of two females from Troop C2A: On October 30, 1998, two adult females (*KM* and *KN*) and one infant (*KN-98* ♀) were evicted by members of Troop C2A. On November 9, 1998, they were observed near the dormitory at Ankoba. Then, they disappeared from the study area. In February 1999, they came up to the study area and began following Troop C2A. Eventually, they returned to the troop.

Thus, at the end of the study (September 1, 1999), six troops (T2, T1, C2A, C2B, C1, and CX) inhabited the study area (Fig. 4). In addition, five troop divisions occurred around the study area: (1) In 1990, four adult females (SN-group) were evicted from Troop B, and they invaded Troop W home range. Troop W was composed of two adult females (*IDO* and *NID*) and one adult male (*KOE*). The four females of the SN-group fought with and dominated over two adult females of Troop W, and eventually the group melted into one; (2) Troop A divided into Troop A1 and Troop A2 in 1992 (for details, see HOOD & JOLLY, 1995); (3) Troop D divided into Troop D1 and Troop D2 in 1993; (4) Troop E divided into Troop E1 and Troop E2 in 1994; and (5) Troop W divided into Troop W1 and Troop W2 in 1996. The females of Troop W1 were the former SN-group and its offspring, whereas those of Troop W2 were *IDO*, *NID*, and their daughters.

Troop Size and Composition

Pooled data showed that the mean troop size was 16.0 ± 7.0 with a maximum troop size of 28 (Troop T1 in 1993). Troop fissions or evictions tended to occur in large-sized troops (Fig. 5a), and they may have resulted from female competition over local resources. All cases of troop fissions occurred in troops with 20 or more non-infant individuals (in 19 troop-years in total). On the other hand, no troop divisions or evictions occurred among smaller troops with 19 or less non-infant individuals (33 troop-years). It is possible that the cost of within-troop competition over food resources increases in large-sized troops.

The number of adult males per adult female was occasionally low in the newly formed troops (i.e. Troops T2, CX, and C2B in Fig. 5b), although the adult sex ratio of the study population was nearly 1:1 (Table 1). This is possible due to hesitation of the male to immigrate into the newly formed small troops. In fact, in the case of the HSK-Group, no males joined the small group of a mother and her two daughters, and this group eventually left the study area.

In the study area, non-adult lemurs occupied about one-third of the whole population [(d) in Table 1], but the proportion of non-adult animals fluctuated in each troop during the study period (Fig. 5c). In particular, newly formed small troops contained a few non-adult individuals (Fig. 5c). This may be because immature offspring did not always follow their mothers, differing from the reported cases of troop divisions for Cercopithecine species (KOYAMA, 1970). In addition, the low birth rate and high infant mortality of small-sized troops may be responsible for the low proportion of non-adult individuals (TAKAHATA et al., unpubl. data).

It seems that upon an increase in the troop size, the troop tends to split into smaller troops, or some females are evicted from it (Table 4 & Fig. 5a). In these cases, several females with their

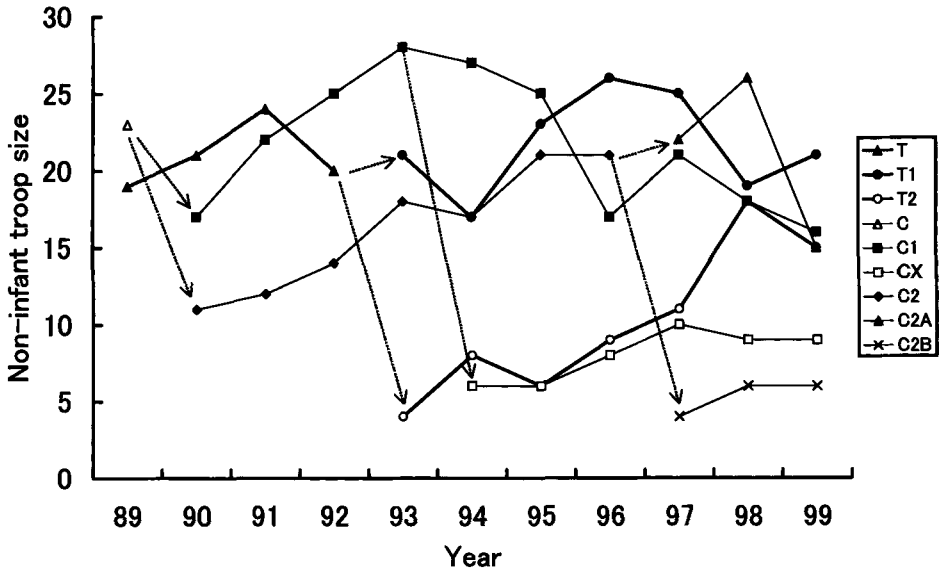

Fig. 5a. Changes in non-infant troop size during the study period. Dotted arrows show troop fission or eviction.

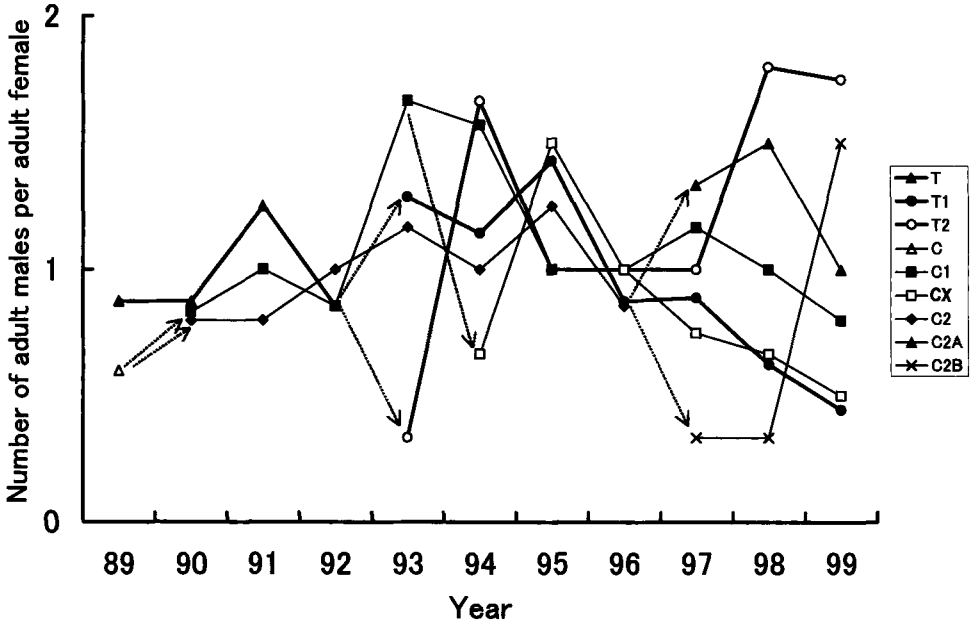

Fig. 5b. Changes in the number of adult males per adult female in each troop.

offspring were evicted from their troops, as a result of persistent targeted aggression by other females. Then, some males joined that female group, forming a new troop. Finally, they established their own home range. Out of five evictions, one resulted in troop formation, and two in troop fusion (i.e. the formation of Troop CX). In another case, the HSK-Group emigrated from the study area, and three females and one infant could rejoin their troops (Table 4).

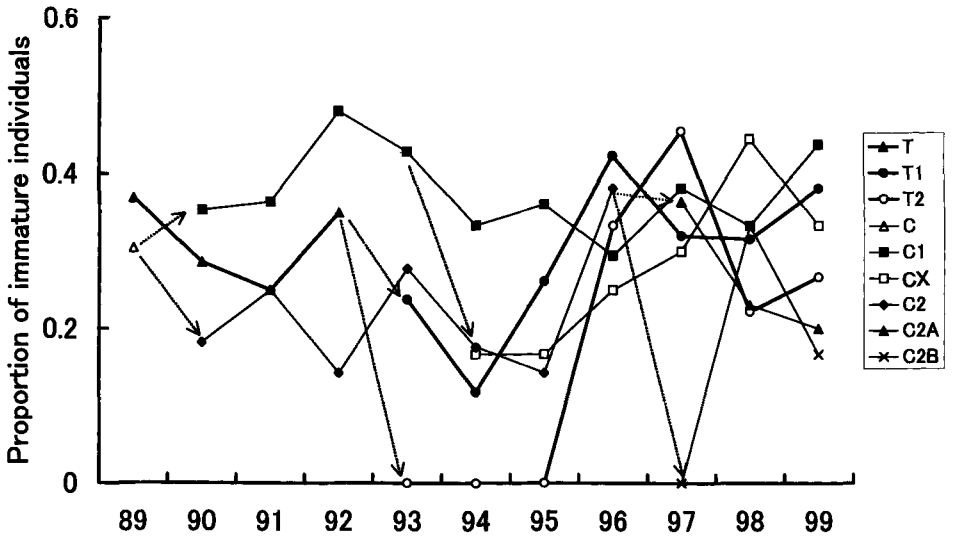

Fig. 5c. Changes in the proportion of immature individuals in each troop.

POPULATION DYNAMICS OF RING-TAILED LEMURS OF KNOWN AGE

Female Survival and Male Presence in Troops

Out of 204 newborn infants, 58 were still alive within the study area on September 1, 1999 (Table 5). Figure 6 shows the survival curves for females and males in the troops. In this figure, we treated 27 individual lemurs (sex unknown) as 12 females and 15 males, based on the sex ratio at birth (81:96).

About 60% of newborn infants survived up to the age of 2, with no sex difference in the rate of survival (first year: χ^2=0.670, p>0.43; second year: χ^2=0.140, p>0.05). Males began to emigrate from their natal troops after the age of 2, and all of them left their troops by the age of 5. Since most of the males eventually disappeared from the study area, it is inappropriate to compare the curve of males with those of females after the age of 2.

For females, the survival rate was 0.465 and 0.446 at the ages of 3 and 4; i.e. about half of the newborn females survived to adulthood. Then, the mortality rate was rather low (4.2 to 20%) for adult females (Table 6 & Fig. 6). At the age of 9, the survival rate of females was 0.174. There was only one female (*ME-89* ♀) who reached the age of 10 yr. The survival curve is incomplete since seven old females were still alive and their ages were estimated to be >13 yr.

Immigration, Emigration, and Length of Tenure for Natal Males

Fifty-seven cases of emigration by natal males were recorded (Table 7). Since some males emigrated two or three times, these emigrations actually involved only 46 natal male lemurs. The males left their natal troops at 2 to 4 yr of age. Out of 46 first emigration, 21 (46%) occurred between the ages of 2 – 3 yr, 22 cases (48%) between the ages of 3 – 4 yr, and two cases (4%) between the ages of 4 – 5 yr. Only one case (2%) emigrated at the ages of 1 – 2 yr.

Table 5. Number of immigration, death, and emigration according to age and sex.

	Name of troop	Infant			Juvenile			Subadult		Adult		Sub-total			Total
		Female	Male	?	Female	Male	?	Female	Male	Female	Male	Female	Male	?	
Immigration	C2/C2A	1	0	0	0	1	0	0	1	10	19	11	21	0	32
	C2B	0	0	0	0	0	0	0	0	3	4	3	4	0	7
	C1	0	0	0	0	0	0	0	0	0	17	0	17	0	17
	CX	1	1	0	0	1	0	2	0	4	6	7	8	0	15
	T/T1	0	0	0	0	0	0	0	1	0	13	0	14	0	14
	T2	0	0	0	0	0	0	0	0	3	13	3	13	0	16
	HSK-G	1	0	0	0	0	0	0	0	2	0	3	0	0	3
	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	U2	0	0	0	2	2	0	0	0	5	3	7	5	0	12
	Total	3	1	0	2	4	0	2	2	27	75	34	82	0	116
Death	C2/C2A	5	8	10	5	1	0	0	0	3	1	13	10	10	33
	C2B	1	0	0	1	0	0	0	0	1	1	3	1	0	4
	C1	1	5	4	1	1	0	2	2	6	0	10	8	4	22
	CX	3	2	1	0	1	0	0	0	5	0	8	3	1	12
	T/T1	6	7	9	1	0	3	3	0	4	1	14	8	12	34
	T2	1	4	2	0	0	0	1	0	1	0	3	4	2	9
	HSK-G	1	0	0	0	0	0	0	0	0	0	1	0	0	1
	B	3	3	1	1	0	0	0	0	0	0	4	3	1	8
	U2	0	0	0	0	0	0	1	1	0	0	1	1	0	2
	Total	21	29	27	9	3	3	7	3	20	3	57	38	30	125
Emigration	C2/C2A	1	0	0	0	0	0	0	3	6	22	7	25	0	32
	C2B	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C1	1	1	0	1	2	0	2	13	8	32	12	48	0	60
	CX	0	0	0	0	0	0	0	1	0	4	0	5	0	5
	T/T1	1	0	0	0	0	0	0	11	5	21	6	32	0	38
	T2	0	0	0	0	0	0	0	0	0	8	0	8	0	8
	HSK-G	1	0	0	0	0	0	0	0	2	0	3	0	0	3
	B	0	0	0	3	1	0	1	1	8	3	12	5	0	17
	U2	0	0	0	2	0	0	1	0	6	4	9	4	0	13
	Total	4	1	0	6	3	0	4	29	35	94	49	127	0	176

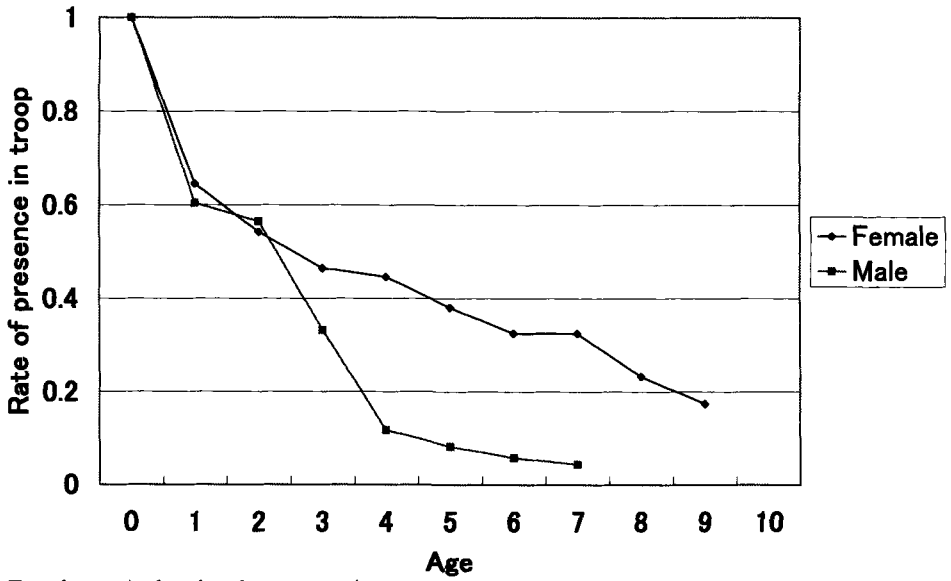

Fig. 6. Female survival and male presence in troops.

In this case, an orphan male (*CW-92*♂) emigrated from Troop C1 to the neighboring Troop CX at the age of 1 yr and 2 months. When he emigrated, his elder sister (*CW-90*♀) was alive in Troop CX. Then, before reaching the age of 3, he left Troop CX and moved into the neighboring Troop A2.

Out of the nine cases of the second transfer, two cases (22%) occurred at the age of 3 – 5 yr, four cases (44%) between the ages of 5 – 7 yr, and three cases between the ages of 7 – 9 yr. Only two cases of the third transfer were recorded, and such moves occurred between the ages of 4 – 7 yr. In about one-third of the first emigration (16/46, 34.8%), natal males moved into neighboring troops. As for the second transfer, four males (44.4%) emigrated into neighboring troops. As for the third transfer, both males may have emigrated to other troops outside the study area.

Forty-three cases of tenures were recorded for the 33 non-natal males who immigrated into a troop then left that troop (Table 8). Ten males transferred twice. Non-natal males changed troops after a tenure varying from 1 to 7 years. The mean tenure was 3.1 ± 1.7 years, the median was 3 years, and the mode was 1 year.

Longevity

At Beza Mahafaly, SUSSMAN (1991) stratified age into eight classes, including infant, 1-yr-old, 2-yr-old, young adult (3 – 4-yr-old), young prime, prime adult, and old. However, the longevity of ring-tailed lemurs is still unknown. SUSSMAN (1992) reported that in captivity, the longest longevity for ring-tailed lemurs was about 23 years, but adults rarely lived past 20 years. In our study population, several females lived at least past 13 years. On the other hand, based on the data shown in Figure 6, it seems to be very difficult for wild ring-tailed lemurs to live long.

Male longevity is also unknown. During the preliminary study in 1988, a juvenile male named *OT* was observed in Troop A. At the age of 3 – 4 yr, he moved from his natal Troop A to

Table 6. Cumulative number of lemurs by BIDE and by age-sex.

	Age class	Infant	Juvenile	Subadult	Adult								
	Years	0	1	2	3	4	5	6	7	8	9	10	11	Total
Female														
	Birth/alive	81	60	42	30	24	17	12	10	5	3	1	0	81
	No. of immigration	2	0	3	3	0	0	1	0	0	0	0		9
	Death	21	8	5	2	1	1	1	2	1	0	0		42
	No. of emigration	2	4	3	2	2	1	0	0	0	0	0		14
	Not reached		0	6	7	5	4	3	2	3	1	2	1	34
Male														
	Birth/alive	96	67	59	34	12	7	5	3	0	0	0	0	96
	No. of immigration	1	1	7	5	1	1	0	0	0	0	0		16
	Death	29	3	4	0	0	0	0	0	0	0	0		34
	No. of emigration	1	1	20	22	3	2	1	2	0	0	0		54
	Not reached		0	5	8	5	3	1	1	1	0	0	0	24
Sex unknown														
	Birth	27	0	0	0	0	0	0	0	0	0	0		27
	Death	27	0	0	0	0	0	0	0	0	0	0		27
Total birth/alive		204	127	101	64	36	24	17	13	5	3	1	0	204
Total immigration		3	1	10	8	1	1	1	0	0	0	0		25
Total death		77	9	9	2	1	1	1	2	1	0	0		103
Total emigration		3	7	23	24	5	3	1	2	0	0	0		68
Not reached			0	11	15	10	7	4	3	4	1	2	1	58

Table 7. Age at transfer by natal males.

Males	Birth year	Natal troop	First transfer		Second transfer		Third transfer	
			Age (yr)	Troop	Age (yr)	Troop	Age (yr)	Troop
HI-89 ♂	1989	C1	2-3	D	6-7	E1		
MW-89 ♂	1989	C1	2-3	D	6-7	E1		
KAT-89 ♂	1989	T	2-3	?				
HIT-89 ♂	1989	T	2-3	?				
MW-90 ♂	1990	C1	3-4	A2	8-9	?		
HI-90 ♂	1990	C1	3-4	C2	7-8	?		
SH-90 ♂	1990	C1	3-4	?				
ME-90 ♂	1990	C1	3-4	?				
MI-90 ♂	1990	C2	3-4	?				
MW-912 ♂	1991	C1	4-5	C2	7-8	?		
MK-91 ♂	1991	C1	3-4	?				
ME-91 ♂	1991	C1	3-4	?				
CW-91 ♂	1991	C1	3-4	?				
MAY-91 ♂	1991	T	2-3	C2	4-5	C1	6-7	?
HIT-91 ♂	1991	T	4	?				
CW-92 ♂	1992	C1	1-2	CX	3-4	A2	4-5	?
ME-92 ♂	1992	C1	3-4	?				
KI-92 ♂	1992	C2	3-4	CX				
MI-92 ♂	1992	C2	3-4	?				
KUB-92 ♂	1992	T	3	?				
MK-93 ♂	1993	C1	2-3	C2	5-6	?		
ME-93 ♂	1993	C1	2-3	C2				
SH-93 ♂	1993	C1	2-3	C2	5-6	?		
HI-93 ♂	1993	C1	2-3	?				
MW-94 ♂	1994	C1	3-4	?				
ME-94 ♂	1994	C1	3-4	?				
SH-94 ♂	1994	C1	3-4	?				
OD-9094 ♂	1994	C2	2-3	T1				
HIT-90194 ♂	1994	T1	2-3	?				
KUB-9094 ♂	1994	T1	2-3	?				
KUB-94 ♂	1994	T1	2-3	?				
MW-95 ♂	1995	C1	3-4	?				
MI-95 ♂	1995	C2	2-3	?				
OD-9095 ♂	1995	C2	2-3	?				
MI-9195 ♂	1995	C2	3-4	?				
OD-95 ♂	1995	C2	3-4	?				
OD-9295 ♂	1995	C2	3-4	?				
KI-95 ♂	1995	C2	3-4	?				
KUB-95 ♂	1995	T1	2-3	T2				
KUB-9095 ♂	1995	T1	2-3	T2				
HSK-95 ♂	1995	T1	2-3	T2				
KYA-90195 ♂	1995	T1	3	?				
MAY-95 ♂	1995	T2	3	?				
ME-899396 ♂	1996	C1	2-3	C2B				
HI-96 ♂	1996	C1	2-3	C2B				
MK-9296 ♂	1996	C1	2-3	?				

Troop C1. At the age of 9 – 10 yr, he again moved from Troop C1 to Troop C2. In 1998, when he was 11 yr old, he was outranked by 5-yr-old male *ME-93* ♂, and ranked the third (first: *DEK*; and second: *ME-93* ♂). This rank reversal might have been due to his senility. He died in late October 2000, aged 13 yr. To our knowledge, this is the first recorded example of a male living in the wild whose longevity exceeded ten years.

Table 8. Tenure and transfer by non-natal males.

	First stay				Second stay				Third stay	
		Year		Tenure		Year		Tenure		Year
Males	Troop	Immigration	Emigration	(yr)	Troop	Immigration	Emigration	(yr)	Troop	immigration
WK	C2	October 1989	1992-1993	3	W	1992-1993				
DS	C2	October 1989	1993-1994	4	C1	1993-1994	1998-1999	5	A2	1998-1999
NE	C2	1989-1990	1992-1993	2	A1	1992-1993				
CH	C1	1989-1990	1994-1995	5						
AB	C1	1989-1990	1991-1992	2						
MG	C1	1989-1990	1990-1991	1						
MC	C1	1989-1990	1996-1997	7						
KAL	T	1990-1991	1991-1992	1						
UDA	T	1990-1991	1993-1994	3	T2	1993-1994	1994-1995	1	U1	1994-1995
UHO	T	1990-1991	1993-1994	3	T2	1993-1994	1995-1996	2	U2	1995-1996
JOU	T	1990-1991	1992-1993	2	T2	1992-1993	1997-1998	5	U2	1997-1998
SS	C2	October 1990	1993-1994	4	C1	1993-1994	1996-1997	3	A2	1996-1997
NU	C2	1991-1992	1994-1995	3	C1	1994-1995	1995-1996	1	A2	1995-1996
NT	C2	1991-1992	1996-1997	5	C2B	1996-1997	Alive	3+		
TJ	C1	1991-1992	1998-1999	7	C2B	1998-1999	Alive	1+		
HK	C1	1991-1992	1994-1995	3						
DA	C2	1992-1993	1996-1997	4	T1	1996-1997	1998-1999	2	?	
DB	C2	1992-1993	Alive	7+						
BET	C2	1992-1993	Died	–						
HMS	T	1992-1993	1997-1998	5	T2	1997-1998	Alive	2+		
SPO	T	1992-1993	1997-1998	5	T2	1997-1998	Alive	2+		
NME	T	1992-1993	Alive	7+						
KIT	T	1992-1993	1997-1998	5	T2	1997-1998	Alive	2+		
SJU	T	1992-1993	1996-1997	4						
KOU	C2	1993-1994	1995-1996	2	C1	1995-1996	August 1998	2	?	
HOS	CX	1993-1994	1993-1994	1						
β	CX	1993-1994	1994-1995	1						
KUR	CX	1993-1994	1997-1998	4	C1	1997-1998	June 1999	1	?	
TRA	T1	1993-1994	1997-1998	4	T2	1997-1998	1998-1999	1	?	
TON	T2	1993-1994	1997-1998	4	U2	1997-1998				
NAS	T2	1993-1994	1994-1995	1	U1	1994-1995				
DEK	C2	1994-1995	Alive	5+						
BON	C2	1994-1995	1996-1997	2						
HTS	CX	1994-1995	1995-1996	1						
HAS	CX	1994-1995	October 1999	5						
PTR	T1	1994-1995	Died	–						
INT	T1	1994-1995	Alive	5+						
TAT	T2	1995-1996	(1999)	4	T1	(1999)	Alive	0+		
LN	C2	1997-1998	(1999)	2	T1	(1999)	Alive	0+		
STO	C1	1997-1998	Alive	2+						
WKO	C1	1997-1998	Alive	2+						
HTO	C1	1998-1999	Alive	1+						
AKM	C1	1998-1999	Alive	1+						

DISCUSSION

Population Changes at Berenty Reserve

In our main study area, the population density reached 4.4 – 5.8 lemurs/ha, probably because this area is the richest area of the Berenty Reserve (Koyama et al., 2001). Jolly et al. (2002) reported that the non-infant population in the scrub area of this Reserve ranges from 1 to 1.5 lemurs/ha, and 2 lemurs/ha in the gallery forest. They also pointed out that there is a difference

in troop size among the habitats: the troop size was largest in the Tourist area (i.e. a part of our study area), and smallest in the scrub area.

During the 10-year study period, the lemur population in our study area increased by 2.7%/year, although the annual growth rate fluctuated from −22.2% to 25.9%. Interestingly, 77.9% of the population increase was due to new births while 22.1% was due to immigration. On the other hand, 51.4% of the population decrease was due to deaths and 48.6% to emigration. Such population increase may have resulted from (1) social changes (e.g. troop division, eviction of females from troop, takeover of other troop's range), (2) natural environmental changes (e.g. drought) as reported in Beza Mahafaly (GOULD et al., 1999), and (3) improved nutritional and water conditions (KOYAMA et al., 2001; JOLLY et al., 2002). Interestingly, JOLLY et al. (2002) pointed out that the population of the gallery forest also increased in the same years, but that the population of spiny desert did not. Thus, the high population density in our study area may be partly due to the food provided by tourists and the water provided by the reserve management.

Our data demonstrated that more individual lemurs, in particular males, emigrated from this population rather than immigrated into this population, just like "resource" rather than "sink." Thus, the artificial high population may bias population structures around the "Tourist Front."

ARE FEMALE LEMURS PHILOPATRIC OR NOT? LIFE HISTORY OF FEMALE LEMURS

The population dynamics of ring-tailed lemurs in our study area might be similar to that of Cercopithecines, specifically the macaques, which form multi-male multi-female social groups (JOLLY, 1966; KOYAMA, 1991; but see KAPPELER, 1999), in particular the female-bonded or matrilineal group defined by WRANGHAM (1980) and ITANI (1985). On the other hand, there were marked and frequent social changes, such as troop division and eviction. Unlike macaques, daughters of lemurs do not rank immediately below their own mothers (NAKAMICHI & KOYAMA, 1997). The occurrence of frequent social changes may reflect the dominance rank system of lemurs.

At Berenty, females did not move between troops as frequently as males, although many females left their original troops due to troop divisions or eviction as seen in the SH and HSK groups. Since the latter two groups were composed of a mother and her daughters, kinship relations among females may have affected the mode of female transfer. Such social changes may have resulted from competition among females, just like the schema of the evolution of female-bonded troops illustrated by WRANGHAM (1980) and VAN SCHAIK (1983).

All cases of troop divisions or evictions occurred in larger troops consisting of ≥20 lemurs (Fig. 5a), and three adult females (*KI*, *KM*, and *KN*) and one infant (*KN-98*♀) could rejoin their troops. In other words, all cases of troop divisions or evictions occurred in large troops containing ≥6 adult females (Table 4). In large troops, first, several females were persistently attacked by dominant females, and were then evicted from the troops. When some males joined such a female-group, a new troop was formed. There were two types of troop formation. The first type was that before establishing a new home range, some adult males joined the female group (e.g. Troop T2). The second type was that only after the establishment of a new home range, some adult males joined the female group (e.g. Troop C2).

During the present study, two cases of eviction resulted in takeovers of ranges/troop fusions in which a female-group invaded another troop, dominated their females, and then joined

together into one. Similar cases were observed among toque macaques (DITTUS, 1986, 1987). On the other hand, in 1998, a clear case of female transfer was observed; two adult females (*KM* and *KN*) from an unknown troop (probably Troop D2) joined Troop C2A. There is a fair possibility that they had been evicted from other troops, but could not establish a range, or a relationship with males. Because of severe inter-troop competition (JOLLY et al., 2002), these lemurs might have been forced to immigrate to the C2A troop. Similar cases were reported for savanna monkeys (HAUSER et al., 1986) and for Japanese macaques (TAKAHATA et al., 1994) (for a review of female transfer, see also MOORE, 1984). However, a question remains: "Why did the females accept such non-related females at the cost of increased troop competition over resources? " In particular, in the case of *KM* and *KN*, the females of Troop C2A had evicted three adult females (*RH, MI*, and *MI-91* ♀) in the previous year. Unfortunately, we do not have a clear answer to this question.

It is noteworthy that although immigration and emigration accompanied with social changes did occur, females were the core of the troop and they stayed in their home-range area. In contrast, males played no apparent role prior to troop division, as KOYAMA (1991) has pointed out. Although promoted by an increase in population, frequent emigrations of females from original troops and several cases of female transfer are the characteristics of ring-tailed lemurs at Berenty, and the females of ring-tailed lemurs should be regarded as philopatric.

LIFE HISTORY OF MALES AND THEIR MOVEMENT

In the study population, all males over 5 yr of age left their natal troops. Most of them emigrated at the age of 2 – 4 yr, just around puberty. SUSSMAN (1992) reported that, at Beza-Mahafaly Reserve, young males emigrated from their natal group at the age of 3 – 5 yr. Then, the males joined other troops, just as reported for Cercopithecine males (NORIKOSHI & KOYAMA, 1975; COLVIN, 1986; MEHLMEN, 1986; MENARD & VALLET, 1996; SPRAGUE, 1998). In this study, the mean male tenure was about three years at Berenty. This figure is similar to the data of 2.8 years reported at Beza Mahafaly (SUSSMAN, 1992). Since their lifetime span was shorter than Cercopithecine males, they changed troops about four times during their whole life span. On the other hand, the mean tenure of non-natal males (about three years) may correspond to the puberty of females. Puberty may occur around 26 months at Berenty (PEREIRA, 1995), and 2.5 years at Beza Mahafaly. Thus, frequent male transfer might result in the avoidance of inbreeding, as pointed out by ITANI (1985).

At the time of their first migration, about one-third of the male ring-tailed lemurs moved to neighboring troops, and about two-thirds settled into areas remote from their natal troops. At the time of their second move, males settled into a remote area, as reported for the savanna monkeys (CHENEY & SEYFARTH, 1983) and Japanese macaques (SPRAGUE, 1998; SUZUKI et al., 1998). On the other hand, some males, such as *OT, HI-89* ♂, and *MW-89* ♂, did not move to a remote area, but rather stayed around their natal troops. Such male lemurs may spend all their life within an area not more than several hundred meters from their natal troops.

Our data suggest that males who emigrate to non-natal troops attain a higher dominance rank in accordance with increased age, especially around the age of 6 to 7 yr (KOYAMA et al., unpubl. data). The length of tenure in troops also affected acquisition of a higher dominance rank. However, the present data is still too fragmentary to analyze the whole life history of male ring-tailed lemurs. Further long-term studies are needed to understand the life histories of this population.

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