DECREASE IN THE BODY MASS OF WILD RINGTAILED LEMURS AT BERENTY RESERVE IN MADAGASCAR WITH ENVIRONMENTAL CHANGES

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ABSTRACT We measured the body mass of 76 (in 2006) and 73 (in 2011) wild ringtailed lemurs (*Lemur catta*) inhabiting the Berenty Reserve in Madagascar. Compared with the data recorded in 1999 (Koyama et al., 2008), the mean body mass of the adults had decreased significantly. In 2006, the adult females had decreased from 2.27 kg to 1.98 kg, and the adult males from 2.22 kg to 2.03 kg. In 2011, the body mass of both adult males and females was still 1.99 kg. In 2011, the group variations in body mass may have expanded. No sexual difference was observed in body mass, similar to the data from 1999. Despite their reduced body mass, adult females maintained a high birth rate (73.0% annually), but infant mortality was very high (86.2%) from 2006 to 2011. We discuss these phenomena with reference to environmental changes in this reserve.

Key Words: Body mass; *Lemur catta*; Primates; Environmental changes; Food availability; Inter- and within-species competition.

INTRODUCTION

Apart from small nocturnal species (e.g., *Microcebus rufus*) (Randrianambinina et al., 2003), few data are available on the body mass of the wild prosimian population. We have been conducting a socio-ecological study on wild ringtailed lemurs (*Lemur catta*) in our study area (14.2 ha) at Berenty Reserve in Madagascar since 1989, based on individual identification (Koyama et al., 2002; 2005).

In November 1999, we captured 101 ringtailed lemurs to collect blood samples for genetic analyses (Koyama et al., 2008). We measured their body mass and found (1) no sexual differences: the mean body mass of the adult females was 2.27 kg, whereas that of the adult males was 2.22 kg. (2) The higher ranked adult males tended to be heavier than the lower ranked males, but no consistent correlation was noted between the body mass of females and their rank. (3) A small difference in body mass was detected among the study groups.

In 2006 and 2011, we captured 76 and 73 lemurs, respectively, to gather genetic data. We measured their mean body mass and found that the body mass of adult lemurs had decreased to about 2 kg. In this report, we discuss the cause of the body mass decrease in our study population with reference to environmental and social changes.

METHODS

A wild population of ringtailed lemurs at Berenty Reserve in Madagascar has been studied by Allison Jolly and her colleagues since the 1960s (see Jolly et al., 2002; 2006 for the study history and details of this reserve). In 1989, we set up a 14.2-ha study area where we identified all ringtailed lemur individuals (Koyama et al., 2002; 2005).

In 1989, the study population consisted of three groups, with a total of 63 individual lemurs (Table 1). The population gradually increased to 116 lemurs in 2006, but decreased to 43 individuals in 2011. This may have been due to several factors; e.g., environmental changes (Koyama et al., 2006), the discontinuation of the artificial water supply by the reserve office, and/or competition with brown lemurs (*Eulemur fulvus rufus*, *Eulemur f. collaris*, and their hybrid) that were artificially introduced in 1975 (Jolly et al., 2006; Rambeloarivony & Jolly, 2013).

Table 1. Non-infant population size of the study population

Year	1989	1990	1991	1992	1993	1994	1995	1996	1997
Adult female (≥3 years old)	26	19	20	25	28	27	28	27	31
Adult male (≥3 years old)	16	16	21	21	30	33	34	25	30
Subadult female (2 years old)	3	1	2	6	6	3	2	4	6
Subadult male (2 years old)	4	5	4	7	7	6	4	7	12
Juvenile female (1 year old)	5	4	6	7	6	2	5	6	7
Juvenile male (1 year old)	6	4	5	7	7	4	8	12	7
Juvenile (1 year old, sex unknown)	3	0	0	0	0	0	0	0	0
Total (non-infant population)	63	49	58	73	84	75	81	81	93

1998	1999	2000	2001	2002*	2003	2004	2005	2006	2007	2008	2009	2010	2011
35	30	34	35	-	39	38	43	46	37	34	33	30	20
35	26	32	32	-	26	36	40	45	36	23	24	21	19
4	7	6	8	-	9	6	4	5	6	4	2	1	0
6	8	5	2	-	5	8	11	3	3	2	4	1	0
12	6	9	11	-	6	4	5	7	6	2	4	0	1
8	5	3	6	-	9	11	4	10	2	4	2	0	3
0	0	0	0	-	0	0	0	0	0	0	0	0	0
100	82	89	94	-	94	103	107	116	90	69	69	53	43

*no data for 2002.

In the present study, we measured 76 individuals (including newborn infants) from seven groups captured in 2006 (Troops C1, C2A, CX, T1A, T1B, T2, and YF) and 73 individuals from seven groups captured in 2011 (Troops C1, C2A, CX, T1, YF, A1, and A2). We compared these data with those of the 95 individuals captured in 1999 from six groups (Troops C1, C2A, C2B, CX, T1, and T2) (Koyama et al., 2008). The ages and matrilineal kin relationships of the individuals born in Troops C1, C2A, C2B, CX, T1, and T2 were known. Troops A1, A2, and YF ranged around our study area, and their ages and matrilineal kin relationships were uncertain.

The lemurs were anesthetized with ketamine hydrochloride using blowpipes and darts, or trapped to collect blood samples for genetic analyses. We grouped the captured individuals into age groups as follows: adults (aged ≥3 years), subadults (aged 2 years), juveniles (aged 1 year), and newborn infants. Births occurred between late August and late December at Berenty (Koyama et al., 2001). In 1999, all births occurred before the date of capture. In 2006, the captures were carried out during the birth season, and in 2011, the captures were done before the birth season.

Statistical analyses were performed using Excel 2007 (Microsoft, 2007) and Statistica (StatSoft Inc., 1999). The level of significance was $p < 0.05$ and all tests were two-tailed.

RESULTS

I. Decrease in Body Mass between 1999 and 2011

Significant differences were observed in the body masses of adult individuals captured during 1999, 2006, and 2011 (females: one-way ANOVA, F = 14.913, $p < 0.00001$; males: F = 9.400, $p < 0.001$) (Fig. 1a and 1b). The mean body mass of adult females decreased from 2.27 kg in 1999 to 1.98 kg in 2006 and 1.99 kg in 2011. Similarly, the mean body mass of adult males decreased from 2.22 kg in 1999 to 2.03 kg in 2006 and 1.99 kg in 2011. No sexual differences existed in the mean body mass in 1999 (Mann–Whitney U-test, U = 279.5, z = 1.449, $p > 0.1$), 2006 (U = 162.5, z = 0.919, $p > 0.3$), or 2011 (U = 541, z = 0.177, $p > 0.8$).

Fig. 1c shows a significant difference between subadults in 1999 and 2006 (F = 16.322, $p < 0.001$). Our study population had no subadults in 2011 (Table 1).

Fig. 1d also shows significant differences among juveniles in 1999, 2006, and 2011 (F = 19.315, $p < 0.00001$).

Fig. 2 shows the age (years) and body mass (kg) of the captured individuals in 1999, 2006, and 2011. The data exhibited similar trends (i.e., body mass increased consistently up to the age of 3 years, followed by a growth plateau). The lemurs captured in 2006 and 2011 had a consistently lower body mass than those of the same age captured in 1999.

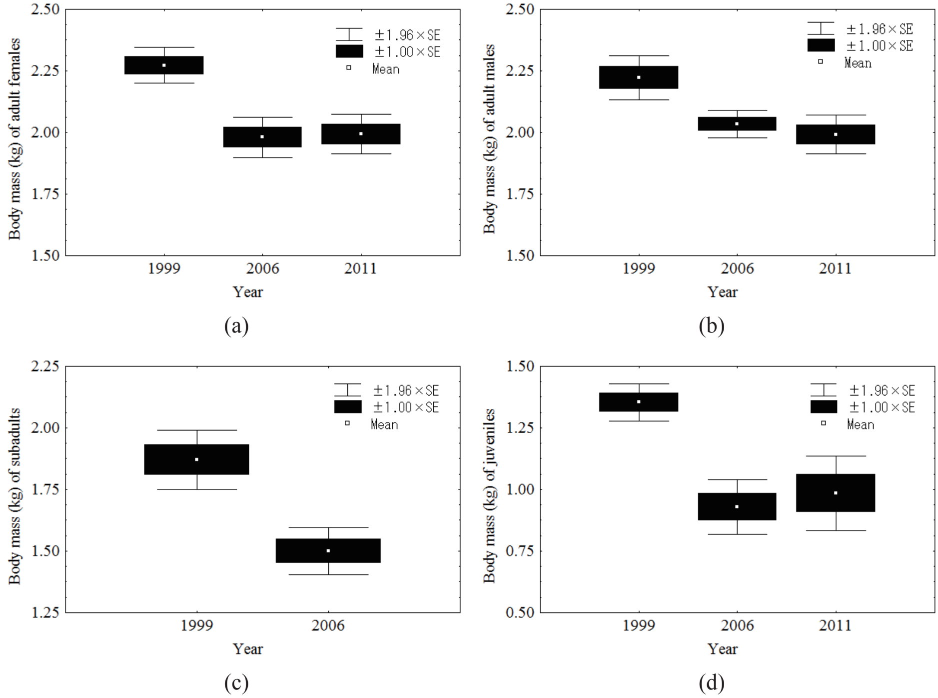

Fig. 1. The body mass of (a) adult females (aged ≥3 years) in 1999, 2006, and 2011, (b) adult males (aged ≥3 years), (c) subadults (aged 2 years), and (d) juveniles (aged 1 year).

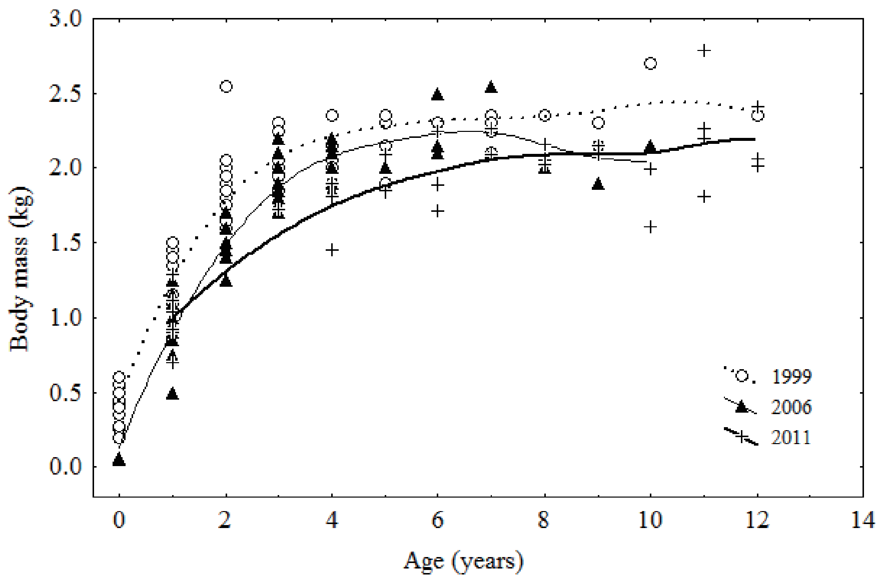

Fig. 2. The ages and body mass (kg) of ringtailed lemurs of known age in 1999, 2006, and 2011, and the least square smoothing curves.

II. Group Differences in Body Mass

In 1999, no significant difference was observed in the mean body mass of adult lemurs among the study groups (one-way ANOVA test, F(5, 48) = 1.28, $p > 0.2$) (Fig. 3a). The post hoc analysis showed a significant difference in the mean body mass of adults between Troop CX and Troop C2B (Duncan's multiple range test, $p < 0.03$). No significant differences were detected in other pairs of groups.

In 2006, no significant difference was noted in the mean body mass of adult lemurs among the study groups (F(6, 43) = 1.85, $p > 0.1$) (Fig. 3b). The post hoc analysis revealed a significant difference in the mean body mass of adults in Troop T1A and T1B (Duncan's multiple range test, $p < 0.04$), but no significant differences were detected in other pairs of groups.

In 2011, a significant difference was observed in the mean body mass of adult lemurs among the study groups (F(6, 60) = 3.585, $p < 0.01$) (Fig. 3c). The post hoc analysis showed that the mean body mass of Troop C2A was significantly higher than that of the other groups (Duncan's multiple range test: vs. C1, $p < 0.01$; vs. CX, $p < 0.01$; vs. T2, $p < 0.05$; vs. YF, $p < 0.01$; vs. A1, $p < 0.05$; vs. A2, $p < 0.01$).

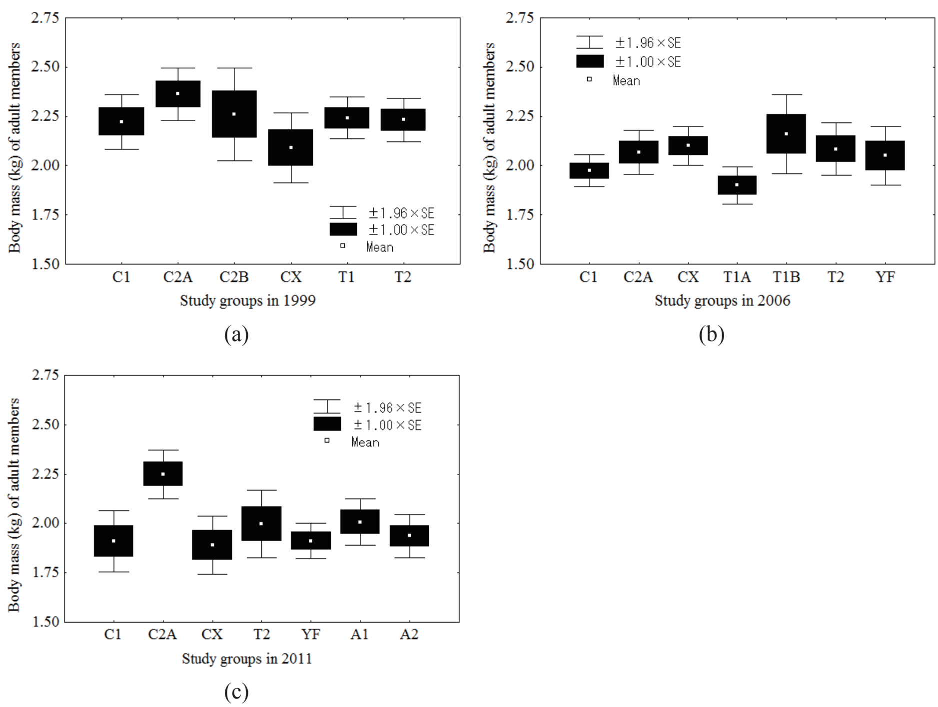

Fig. 3. Mean body mass of adult members in each study group in (a) 1999, (b) 2006, and (c) 2011.

Table 2. Birth and infant mortality rates of the study groups (2006–2011)

	Study groups					
	C1	C2A	CX	T2	YF	Total
No. of females	23	24	20	15	18	100
No. of births	19	19	10	12	13	73
Birth rate (%)	82.6	79.2	50.0	80.0	72.2	73.0
No. of newborn infants	15	14	10	9	10	58
No. of deaths	12	12	10	9	3	50
Infant mortality rate (%)	80.0	85.7	100.0	100.0	70.0	86.2

III. Reproductive Parameters

Despite the decrease in body mass, females retained a high birth rate of 73.0% from 2006 to 2011 (Table 2). This value was not significantly different from the 72.9% recorded for age-known adult females in 1989–1998 (calculated from Table 4 of Koyama et al., 2001) (χ^2 = 0.00, DF = 1, p = 0.9928).

No significant group difference was observed in the birth rate (one-way ANOVA: F = 1.867, p = 0.1227) from 2006 to 2011. However, the post hoc analysis showed a significant difference between Troop C1 and Troop CX (Duncan's multiple range test: p = 0.0394).

The infant mortality was 86.2% from 2006 to 2011 (Table 2). This value was much higher than the 28.6% recorded for age-known adult females in 1989–1998 (calculated from Table 4 of Koyama et al., 2001) (χ^2 = 40.750, p = 0.0000).

No significant group difference was detected in the infant mortality (F = 1.455, p = 0.2291) from 2006 to 2011. The post hoc analysis detected no significant differences among the study groups.

DISCUSSION

I. Decrease in Body Mass

The present study showed that the mean body mass of adult ringtailed lemurs decreased by 12.3% (females) and 10.4% (males) between 1999 and 2011 in our long-term study site at Berenty Reserve in Madagascar (Figs. 1 and 2). The values recorded in 2006 and 2011 were lower than those of the adult females (2.207 kg) and adult males (2.213 kg) recorded in another wild population in the Beza Mahafaly Reserve in Madagascar (Sussman, 1991). No significant differences were observed in the body masses of adult males and females throughout the study period, following Kappeler's (1990; 1991) observations of sexual dimorphism patterns in prosimian primates.

Several possibilities can be considered to explain the decrease in the mean body mass.

(1) Environmental changes may have caused a food shortage. Ringtailed lemurs mainly depend on fruit and young leaves, particularly tamarind (*Tamarindus indica*) fruit (Mertl-Millhollen et al., 2006; Simmen et al., 2006). Our long-term analysis of tamarind trees suggested that the abundance of this species has decreased in our study area (Koyama et al., 2006).

Several possible explanations exist for the decline in the abundance of tamarind trees, including climatic effects (particularly the droughts that occurred in 1983 and 1992), a fall in the underground water level, and the illegal felling of trees. It has been pointed out that global warming has threatened the biodiversity of the lowlands of Madagascar (e.g., Raxworthy et al., 2008). In Berenty, Rambeloarivony & Jolly (2013) also indicated that the water table of Berenty is likely to become progressively lower and less reliable, and they speculated that the predicted scenarios of global warming and a lower water table will exacerbate biological and social stresses on the lemurs.

(2) The toxic component (mimosine) of the seeds of an artificially introduced plant species (*Leucaena leucocephala*) may also have affected the health of the lemurs (Rambeloarivony & Jolly, 2013). In recent years, ringtailed lemurs have allocated a considerable proportion of their time to feeding on several artificially introduced plant species during the dry months, including *L. leucocephala* (Soma, 2006). Crawford et al. (2006) indicated that mimosine (a nonprotein amino acid known to be toxic to mammals, particularly nonruminants) may have caused alopecia in ringtailed lemurs (i.e., "bald lemur syndrome"), although many unresolved questions remain.

In 2004, the reserve office started to remove artificially introduced plant species. However, the cutting of introduced plants may have exacerbated the food shortage for lemurs.

(3) The development of interspecies competition with brown lemurs. In the 1970s, several individuals of the two subspecies of brown lemur (*E. fulvus rufus* and *E. f. collaris*) were artificially induced into Berenty Reserve, and their population increased rapidly (Jolly et al., 2006; Rambeloarivony & Jolly, 2013), which may have led to severe interspecies competition between ringtailed and brown lemurs (Pinkus et al., 2006).

(4) The non-infant population increased from 82 in 1999 to 116 in 2006 in the study area (Table 1). Such a high population density may have promoted severe within-species competition, which caused the decrease in body mass during this period. In contrast, the population size abruptly decreased since 2006 (Table 1), but the mean body mass was still low, which suggests that the study population was still suppressed by factors other than population density (e.g., environmental changes, toxic components, or interspecies competition).

Regrettably, the factors dominant in the decrease of body mass are unknown because we have no veterinary or physiological data for the study population of ringtailed lemurs. We expect to further study this population.

II. Group Variation in Body Mass

Throughout our long-term study, we observed slight group differences in body mass. In 1999, we found a significant difference in the body mass of adult members between the lightest group (CX) and another group (C2B) (Koyama et al., 2008). Troop CX members were also heavily infested with ticks. We suggest that this variation may have resulted from environmental conditions (Troop CX inhabited the most humid area of the gallery forest) and dominance relationships (Troop CX was subordinate to neighboring groups, likely because of their small body size).

In 2006, the mean body mass of most groups decreased to a level similar to that of Troop CX in 1999. A significant difference in the mean body mass of adults was observed only in Troops T1A and T1B. In contrast, the lemurs in Troop C2A maintained their heavier body mass in 2011, but the reason for this is unknown.

A small habitat difference (e.g., food availability of their home range) or group dominance relations may have caused such a group variation in body mass. However, at this point, the dominant factors involved in controlling the group differences remain unknown. Further data will be needed to clarify the relationship among body mass and ecological and social conditions.

III. Birth Rate and Infant Mortality Rate

Notably, the female ringtailed lemurs maintained a high birth rate during 2006–2011 despite the decrease in their body mass. In adapting to the harsh and unpredictable environments of Madagascar (Wright, 1999), ringtailed lemurs may have developed a high reproductive potential.

In contrast to the high birth rate, however, the infant survival rate decreased greatly during 2006–2011. We suppose that this high mortality should be linked to the decrease in body mass, but its proximate mechanism is unknown due to the lack of veterinary and physiological data. In 2007, an artificial water supply to the lemurs was discontinued by the reserve office to control the increase in the brown lemur population (Rambeloarivony & Jolly, 2013), which may have affected the body conditions of the ringtailed lemurs. This increase in infant mortality was probably connected to the decline in the size of our study population.

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