**Original Article**

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# Lifespan and Reproductive Senescence in a Free-Ranging Ring-Tailed Lemur *(Lemur catta)* Population at Berenty, Madagascar

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**Key Words**
Longevity · Lifespan · Life table · Age-specific fecundity · Reproductive lifespan · Reproductive senescence · Postreproductive lifespan · Mortality rate

**Abstract**
The lifespan and age-specific fecundity of female ring-tailed lemurs *(Lemur catta)* were estimated from a 24-year longitudinal dataset based on individual identification at Berenty Reserve, Madagascar. The mean lifespan of females in 10-year (1989–1998) birth cohorts was 4.9 ± 4.9 years (n = 77), and the longest recorded lifespan in the population was 20 years. The mortality rate of adult females increased to ≥20% at 10–11 years old and reached 33–50% at 12–15 years old. Although the birth rate of old females (12–17 years old) was 72.0%, slightly lower than that of prime adult females (4–11 years old), i.e. 80.2%, no significant difference was found between them. Half of the females who reached the age of 12 years gave birth in the last year of their life. The oldest mother to give birth was 17 years old. These results suggest that most females can maintain reproductive performance in their later life and that there is no evidence for a postreproductive lifespan in this species.


## Introduction

A decline in age-specific fertility in later life is not uncommon among mammals [Caro et al., 1995; Pavelka and Fedigan, 1991], although only a handful of species (e.g. humans and short-finned pilot whales) have a long postreproductive lifespan [Co-


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hen, 2004]. Reproductive senescence or menopause with age is an important life history trait for understanding the lifetime reproductive strategy of females, particularly in wild populations where some females stop reproducing before death [Paul et al., 1993]. For ring-tailed lemurs, Sussman [1991] and Parga and Lessnau [2005] reported a decline in the fecundity of old females. In spite of these reports, it is still unclear whether ring-tailed lemurs have a postreproductive lifespan, because of the small sample size and the lack of information on aging in this species.

Data from captive animals suggest a maximum lifespan of lemurs that appears to be relatively long for their body size. As far as we know, the maximum recorded lifespan in a captive ring-tailed lemurs is 37.3 years [Weigl, 2005], which is similar to that of macaques and baboons in captivity. 'The rate of living theory', a theory to potentially explain long-lived mammals (e.g. bats [Brunet-Rossini and Austad, 2004; Wilkinson and South, 2002]), predicts that animals with a low basal metabolic rate are long-lived. The basal metabolic rates of prosimians have been consistently found to be lower than those of anthropoid primates and lower than those predicted by the mass-dependent values of Kleiber and Rogers [1961] for eutherians [Müller, 1985]. Thus, it is reasonable to predict that lemurs have a relatively long lifespan.

In this study, we estimated the lifespan and age-specific fecundity of naturally occurring ring-tailed lemurs from a 24-year longitudinal dataset based on individual identification and examined whether ring-tailed lemurs have a postreproductive lifespan.

## Methods

The present study was conducted at Berenty Reserve in southern Madagascar [Jolly et al., 2006; Jolly, 2012]. In the main study area (14.2 ha) within the reserve, a long-term study based on individual identification has been conducted since 1989 [Koyama et al., 2001, 2002]. Demographic data for 24 years from 1989 to 2013 were used for this study. The population size ranged from 49 to 116, and the number of troops ranged from 3 to 8. More detailed analysis of the population dynamics will be published as another article [Ichino et al., in preparation]. Data for the first 10 years were collected by Koyama and his colleagues [Koyama et al., 2001, 2002]. After 2000, 5 experienced field researchers (Ichino, Soma, Miyamaoto, Sato and Chatani) collected individual data. At Berenty, lemurs are well habituated to humans, and the home ranges of the lemur troops have been stable over a long time [Mertl-Millhollen, 2000; Koyama et al., 2006], enabling the identification of lemurs over the years using only some permanent or temporary characteristics on their faces and bodies. Additionally, other researchers and 2 local field assistants provided further individual information.

We used individual records from September of each year to calculate the length of individual lifespans because ring-tailed lemurs are strict seasonal breeders and the birth season peaks in September at Berenty [Koyama et al., 2001]. For 2002, 2008 and 2010, we have no available individual records from September; therefore, we used data from October for 2008 and 2010, and data from January for 2002. We analysed only data for females, because ring-tailed lemurs live in matrilineal societies and it is difficult to estimate the lifespan of males who emigrate from their natal troops.

Longitudinal demographic data of 10-year cohorts (1989–1998) were analysed. We excluded 4 females of troop U2 from the data set and analysed data of 77 females. In addition to the females, we analysed data of females who were born before 1989. Although it is impossible to know their exact ages, we can estimate their minimum lifespan.

**Table 1.** Life table for female ring-tailed lemurs *(L. catta)* at Berenty

| Age, years | Females, n | Dead or disappeared females, n | Mortality | Survivorship | Life expectancy |
|---|---|---|---|---|---|
| 0 | 77 | 20 | 0.2597 | 1 | 4.8701 |
| 1 | 57 | 11 | 0.1930 | 0.7403 | 5.5789 |
| 2 | 46 | 6 | 0.1304 | 0.5974 | 5.9130 |
| 3 | 40 | 3 | 0.0750 | 0.5195 | 5.8000 |
| 4 | 37 | 4 | 0.1081 | 0.4805 | 5.2703 |
| 5 | 33 | 2 | 0.0606 | 0.4286 | 4.9091 |
| 6 | 31 | 3 | 0.0968 | 0.4026 | 4.2258 |
| 7 | 28 | 4 | 0.1429 | 0.3636 | 3.6786 |
| 8 | 24 | 4 | 0.1667 | 0.3117 | 3.2917 |
| 9 | 20 | 1 | 0.0500 | 0.2597 | 2.9500 |
| 10 | 19 | 4 | 0.2105 | 0.2468 | 2.1053 |
| 11 | 15 | 3 | 0.2000 | 0.1948 | 1.6667 |
| 12 | 12 | 6 | 0.5000 | 0.1558 | 1.0833 |
| 13 | 6 | 3 | 0.5000 | 0.0779 | 1.1667 |
| 14 | 3 | 1 | 0.3333 | 0.0390 | 1.3333 |
| 15 | 2 | 1 | 0.5000 | 0.0260 | 1.0000 |
| 16 | 1 | 0 | 0.0000 | 0.0130 | 1.0000 |
| 17 | 1 | | | | |

The infants whose sexes were unknown (n = 27) are not included in this table (see text for details).

## Results

*Maximum Lifespan*

The maximum recorded lifespan of female ring-tailed lemurs in the 10-year birth cohorts was 17 years. Among 77 females, 1 female (OD-9096♀) reached the age of 17 years, and she was still alive at the last census in 2013. The second longest-lived female (ME-8993♀) lived until the age of 15 years. The mean lifespan of the top 10% longest-lived females in the 10-year cohorts was 13.75 years (n = 8).

Among the females who were born before 1989, the longest-lived female's (MI) age was estimated as at least 20 years.

*Mean Lifespan and Life Table*

The mean lifespan of female ring-tailed lemurs in the 10-year cohorts was 4.9 ± 4.9 years (n = 77). The short mean lifespan was the result of high infant mortality. The 1-year mortality rate (from birth to 1 year old) was 26.0% (table 1), which is likely an underestimate, because 27 infants who died whose sexes were unknown were not included in the estimate. The mean lifespan of females who survived their first year was 6.6 years (see table 1 for the life expectancy).

The mortality rate of 1-year-old females was still high, 19.3%, and the rate was consistently low at 2–9 years old. The mortality rate increased again to more than 20% at 10–11 years old, and reached 33–50% at 12–15 years old (table 1).

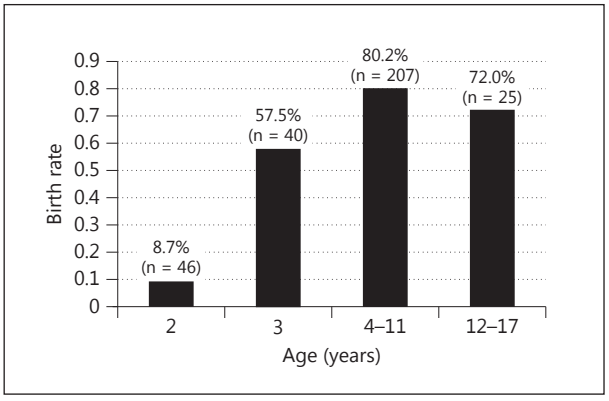


**Fig. 1.** Birth rate of female ring-tailed lemurs *(L. catta)* in each age category based on 10-year birth cohorts (1989–1998).

*Age-Specific Fecundity*

A handful of females started their reproduction at the age of 2 years, and the birth rate was very low, only 8.7%. The birth rate increased to 57.5% at the age of 3 years and reached a plateau at 4 years (fig. 1). Although the birth rate at the age of 12–17 years (72.0%) was slightly lower than that at 4–11 years (80.2%), there was no significant difference between them ($p = 0.43$, Fisher's exact test; fig. 1).

*Last Birth*

Including females who were born before 1989, at least 22 females reached the age of 12 years. Out of them, 11 (50.0%) gave birth in their last birth season before their disappearance, 10 did not give birth, and 1 was still alive. Thus, half of the old females maintained reproductive performance until their disappearance. The oldest mother to give birth was 17 years old. This oldest record might be updated because she was still alive at the last census in 2013.

## Discussion

*Lifespan and Life Table*

The maximum recorded lifespan in this study was relatively long (20 years), although it is much shorter than that from captive records (37.3 years) [Weigl, 2005]. This value is similar to that of ring-tailed lemurs in the Bezà Mahafaly Special Reserve. Gould et al. [2003] suggest that 18–20 years may represent the maximum lifespan for naturally occurring female ring-tailed lemurs. Our demographic data supported their expectation, despite the differences in environmental conditions and population density between the 2 populations [Sussman, 1991; Jolly et al., 2002; Koyama et al., 2002; Gould et al., 2003].

Although the maximum lifespan was relatively long, most females may die earlier in the wild population. The mortality rate of females increased at 10 years and reached a maximum at 12–15 years (table 1). This suggests that somatic senescence of naturally occurring ring-tailed lemurs appeared to start around the age of 10 years which is much earlier than that of the sifakas of Bezà Mahafaly Special Reserve in

which the mortality increased after 19 years [Richard et al., 2002]. Cuozzo and Sauther [2006] found ring-tailed lemurs at Bezà Mahafaly Special Reserve display a much higher frequency of tooth loss than sympatric sifakas and other primates. Tooth loss might cause a dietary shift and result in high mortality of ring-tailed lemurs at a relatively earlier age.

*Reproductive Senescence*

Reproductive senescence is broadly seen in primates and discussed from the viewpoint of the evolution of human menopause [Takahata et al., 1995; Caro et al., 1995; Paul et al., 1993]. This study demonstrated that most females died or disappeared before they experienced significant reduced fecundity, suggesting that there is no postreproductive lifespan for this species. Studies on two wild sifaka populations also suggested no evidence of a postreproductive lifespan [Wright et al., 2008; Richard et al., 2002]. One possible explanation for the lack of a postreproductive lifespan is earlier dental senescence in naturally occurring populations where lemurs have suffered from recent environmental change in Madagascar [King et al., 2005].

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