

Atsalis S, Margulis SW, Hof PR (eds): Primate Reproductive Aging.
Interdiscipl Top Gerontol. Basel, Karger, 2008, vol 36, pp 17–28

Aging in Wild Female Lemurs: Sustained Fertility with Increased Infant Mortality

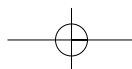
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Jukka Jernvall^d

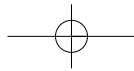
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Abstract

Understanding the way prosimian primates age can be helpful in inferring what the 'basal primate mode' of senescence may have been. Even though prosimians are known to be long-lived in captivity, relatively little is known about their reproductive senescence, and even less is known about how prosimians age in their natural habitats. Twenty years of observational data in Madagascar for four *Propithecus edwardsi* sifaka groups were used to analyze reproductive and behavioral trends of aging in the wild. Techniques using tooth wear were developed to establish ages of wild sifakas and to estimate the onset of their 'dental senescence', a proxy for the onset of decline in the ability to obtain nutrition. Estimated maximum longevity was 32 years for female sifakas. Based on the loss of dental functional morphology, and changes in tooth wear patterns and in chewing efficiency, dental senescence was estimated to set in at approximately 18 years of age. Of the adult females in the study groups, the yearly average of the number of dentally senescent females was 29%. There was no indication of a decline in fertility in the dentally senescent females (aged >18 years) compared to younger adult females (aged 4–18 years). The field data showed, however, that in years when rain was decreased during months of prime lactation, infants of dentally senescent mothers died before weaning. This may be because the nursing mother's worn teeth could not shear leaves and extract moisture, nor nutrition, both essential for successful lactation. Old females showed no clear signs of social disengagement, further suggesting that drought-induced stress plays a direct role in increased infant mortality. These data support earlier findings that prosimian females continue to cycle and give birth until death. The effect of environmental variation on infant survival, however, indicates an incipient age-linked decline in reproductive fitness. Therefore, whereas lemurs represent the condition of no menopause, changes in infant survival may uncover selective factors that have in part led to the evolution of menopause in other primates.

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Since lifetime reproductive success is the currency of evolutionary success, the long post-reproductive lifespans of human females require explanation. Anthropologists have tended to treat humans as unique because they have long maximum life-spans, they exemplify 'life in the slow lane', with females delaying reproduction in many cultures until well past menarche, and adult females experience a prolonged postreproductive life cycle stage [1–3]. Indeed, there is a large literature that attempts to understand the selective underpinnings of longevity in humans, with particular emphasis on the evolution of menopause [2, 4–12]. Increasingly, however, it is understood that the relationship between reproductive and somatic senescence may be complex in many primate species, and that long lifespans are not unique to humans, hominoids, or even anthropoids [13]. The smallest-bodied (and some would argue, most primitive) primates are cheirogaleids (the mouse lemurs and their relatives), and studies in captivity show that mouse lemurs can live almost ten times longer than like-sized nonprimates such as mice or shrews [14]. Larger lemurs, with body sizes of 2–3 kg live for over 30 years in captivity [15]. Understanding the evolution of long lifespan and senescence in humans benefits from a better understanding of these phenomena in the most primitive of our primate relatives.

Field studies concerning primate behavioral gerontology, particularly those focusing on unprovisioned, wild primates, are rare [16–21]; most studies of primate aging have focused on captive or provisioned animals [22–28].

Captive conditions lower requirements for strenuous physical activity [29] and mental function needed for foraging and avoiding predation [30, 31], and they result in slower rate of dental wear in captive animals [32]. Thus, it may be difficult to estimate some of the effects and evolutionary significance of senescence. Long-term studies of primates in their natural habitats, however, can offer important insights into the evolutionary context of senescence, especially reproductive senescence.

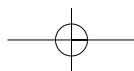
The few studies of aging primates in the wild include baboons, capuchin monkeys, langurs and chimpanzees [18, 20, 21, 33–37]. Data from these studies show a slowing of reproduction of older females, in fact approximately one-quarter to one-third of the lives of female monkeys and apes is nonreproductive [38, 39]. In contrast, in captive lemurs there is no evidence of a slow down of reproduction before death of older females [40]. In addition, in studies of wild lemurs, there is no evidence of cessation of reproduction in older females [15, 41–43].

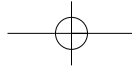
In this chapter we report on a 20-year study of a large-bodied species of lemur, *Propithecus edwardsi*, the Milne Edwards' sifaka, in its natural habitat. Demographic, morphological, and behavioral data were combined to examine the relationship between social and reproductive behavior in old versus young mothers.

Methodology

Study Site and Subject Species

This study of *Propithecus edwardsi* took place in the southeastern rainforest of Madagascar, now part of Ranomafana National Park (21°02'–21°25' S and 47°18'–47°37' E) [44]. The altitude of the





rainforest ranges from 600 m to 1,513 m, and rainfall averages 3,090 mm a year, with half of the rain falling between December and March. Currently, a trail network 30 km in length and covering 2.1 km² in the core study area facilitates research on sifakas and twelve other sympatric lemur taxa.

Propithecus study animals are habituated to human observers and are periodically anesthetically darted, captured, and released [43, 45]. The Milne-Edwards' sifaka, *Propithecus edwardsi* [46], is the largest of 12 lemur species inhabiting the submontane rainforest of Ranomafana National Park, [44]. *P. edwardsi* is an arboreal, diurnal, frugivorous/folivorous, sexually monomorphic lemur that lives in groups of two to nine individuals [47]. Milne-Edwards' sifakas obtain most of their fats and protein from seeds and new leaves [48]. Both sexes may migrate from natal groups, and both males and females have been observed to change groups more than once in their lifetime with some individuals migrating into three different groups over 15 years [47].

The present study focused on up to ten social groups of sifakas located within the boundaries of the park. A field study of *Propithecus edwardsi* was initiated in 1986 and has continued uninterrupted until today. For two decades, Patricia Wright, colleagues and her team of Malagasy research assistants have systematically recorded over each annual cycle the behavioral ecology and demography of this population [15, 49–54]. Inter-observer reliability has been verified throughout the study. Wright chose to study Milne-Edwards' sifakas because they inhabit a continuous rainforest of 43,000 ha to which there is long-term access to continually gather behavioral, phenological, predation and climatic information [45, 55–57]. Thus, there is a substantial long-term database that has allowed us to relate changes across the lifespan to the reproductive output of individual lemurs. On average, 29% of sifaka females have been older than 18 years of age or 'dentally senescent' (showing compromised dental function due to tooth wear).

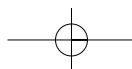
Capture Methods

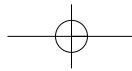
To capture sifakas, our darting team has used a CO₂ air rifle, which launches light-weight 9-mm darts. Darts inject Telazol® at 10 mg/kg of body weight intramuscularly. Animals were captured with large nets as they fell. Each animal was weighed and measured. Newly captured individuals were marked with nylon identifying collars. Dental molds taken of anesthetized animals were used to determine the ages of new individuals, and color-coded collars facilitated behavioral monitoring of individuals over time. The animals were allowed to recuperate in light-weight sacks (recuperation time ~3 h) before release back at the darting site and they were followed to ensure complete and safe recovery. We have used this protocol successfully since 1989 [58].

Estimating Age

Studies of ontogenetic processes are greatly enhanced when the ages of individuals are known, but some of the individuals in our sample were born prior to the initiation of the field study or migrated into our study groups, therefore their precise ages are unknown. To estimate the ages of such individuals we built on the work of King et al. [43] who found that sifaka teeth wear predictably with age.

Dental impressions (Express, low-viscosity, regular set, 3M Dental Products) have been taken of cleaned and dried right mandibular tooth rows of approximately 30–0 anesthetized individual *Propithecus* each year of this research project. New individuals reaching adulthood, or immigrants are added each year to the core set of individuals captured each year. Our analysis focused on only the second molar as all teeth erupt nearly simultaneously in sifakas [59]. High-quality plaster casts (Fugirock GC Europe, Leuven, Belgium) made from the dental impressions were scanned in three dimensions using a piezo scanner (MDX-15, Roland) with 100 µm resolution. Resultant point files were exported to a Geographic Information Systems (GIS) environment (MFWorks 3.0, KeiganSystems, London, Ont., Canada) where digital elevation models (DEMs) were constructed from interpolated (inverse distance weighting) surfaces [60, 61]. Dentine exposed with the wear of





the overlying enamel was visible in DEMs and was delineated and measured using standard GIS tools.

To generate a wear scale, we used a combination of known time intervals between capture dates of repeatedly captured and molded individuals, and known ages for the subset of individuals whose births were recorded in the wild. An important discovery was that the rate of increase of dentine exposure is similar in individuals of different ages (at least until ~ 30 years). Therefore, a linear relationship between tooth wear and age applies. Specifically, King et al. [43] found that the age of female sifakas varied predictably with the square root of the two-dimensional area of exposed dentine on the mandibular second molar [Estimated age (years) = $1.892 + 5.994 X \sqrt{\text{area of exposed dentine}}$; $R^2 = 0.97$]. We used this least-squares regression to estimate the ages of new individuals on the basis of their dental wear. Consequently, we had either known ages or estimated ages for all individuals in our study.

Percentage of Old Females

For each of the four groups each year, we determined the number of reproductive aged females that were old (18–30+ years) versus young (4–17 years). We then determined the number of old versus young females for each sifaka group, for each of the twenty years of the study.

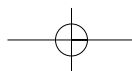
Dental Functional Traits and Food Processing

The dental casts of repeatedly captured sifakas allowed us not only to estimate ages, but also to document and quantify changes in tooth functional characteristics across the long span of adulthood in individual sifakas. Details of the methods employed can be found in King et al. [43] and supplementary information. We used GIS procedures to measure the surface relief of each tooth, with relief defined as the ratio of the 3D surface area to the 2D planometric or 'footprint' area of each tooth crown [61, 62]. We also calculated the average slope across the occlusal surface of each tooth. Finally, we used GIS to delineate and measure mesiodistal shearing crests. We measured both the 3D lengths of the crests and the 2D lengths of their projections onto the xy plane and standardized crest lengths by the mesiodistal lengths of the teeth. A tooth crown with a blade length of two has twice its length in shearing blades.

We documented potential lifespan changes in tooth use by quantifying wear marks on high-resolution epoxy casts of the protoconid cusp [43]. Wear scratch frequencies on enamel were scored from a square that is 0.4 mm on each side at $\times 35$ magnification [63]. Additionally, we examined the size of fragments of readily identifiable rahiaka seeds (*Chrysophyllum boivinianum*) in fecal samples from three dentally 'prime' individuals and one old female with very worn teeth. For each of the three individuals we calculated the proportion of all rahiaka fragments (> 1 mm) that were large (> 2 mm).

Social Behavior

A team of research assistants followed individuals for an average of 8 hours/day over 200 days/year. Using focal animal follows they recorded grooming interactions and nearest neighbors [45, 64]. Weekly group censuses provided accurate demographic information including birthdates and mortality required for examining questions regarding reproductive senescence and maternal investment. We recorded individuals' sleeping partners at dusk as an indication of whether older females are more solitary than younger females. We have analyzed the sleeping partner data for 21 days per female across seven consecutive months (September/October 2004 to March/April 2005). Two old females (estimated 26 and 30 years old) and two young adult females (6 and 12 years old) were compared. Only adult sleeping partners were counted; infants were excluded from the analysis.



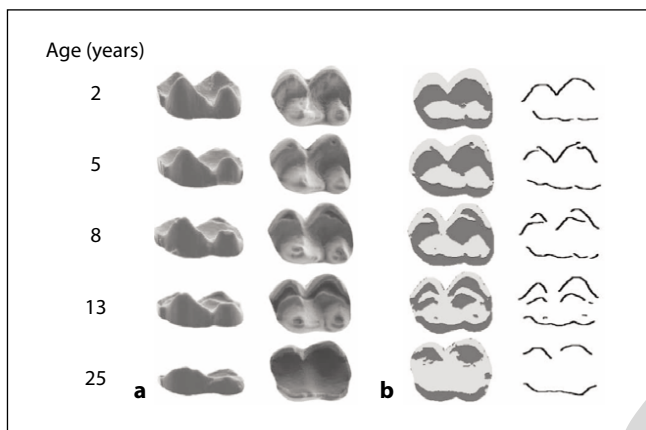


Fig. 1. The effects of wear on sifaka molar teeth. **a** Lingual (left) and occlusal (right) views of a wear series of second mandibular molars. As the enamel wears, underlying dentine (dark) is exposed. **b** GIS analysis of the same teeth identifies shearing crests at the intersection of buccal-facing surfaces (light) and lingual-facing surfaces (dark). In the right column, shearing crests have been isolated for measurement.

Results

Aged Females

How frequent are old individuals in our study sample? Over the 20 years of our demographic study, 33% of the females have consistently been 'old' (between 18 and 30 years) and 29% of the females have been 'very old' (25–30+ years) in any given year. This has been the case at Ranomafana despite the high predator pressure on sifakas from an active population of *Cryptoprocta ferox*, the carnivorous fossa that eats lemurs [52, 55]. Thus, old Milne Edwards' sifaka females may play an important role in population dynamics.

Tooth Wear and Dental Senescence

Unworn molar teeth are high-crowned with sharp, high-relief cusps (fig. 1a). Tooth wear removes surface enamel resulting in more blunted cusps and the exposure of underlying dentine. Newly formed dentine 'pools' are surrounded by sharp enamel edges capable of shearing food particles (fig. 1b). With continued wear, dentine pools increase in size to form crescents on the buccal side and the tooth comes to approximate the selenodont morphology typical of specialized herbivores such as koalas.

We analyzed lifespan changes in potential dental functional traits including tooth crown relief, average crown slope, and mesiodistal shearing crest lengths. We found that tooth crown relief was high in young female sifakas but decreased rapidly, with minimal values attained during early adulthood, by approximately six years of age (fig. 2a). We found similar results for the average slope of tooth crowns. Both crown relief and average

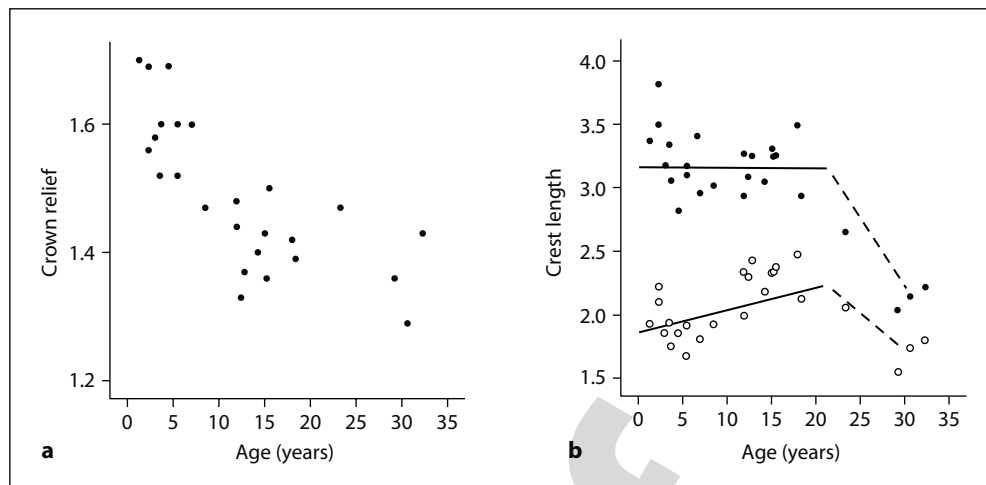
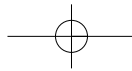
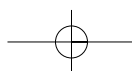


Fig. 2. Dental morphology and tooth wear. **a** Crown relief is high in young female sifakas but is quickly reduced via tooth wear by early adulthood (<7 years). **b** Open circles = 2D shearing crest lengths (mm); filled circles = 3D shearing crest lengths. As wear exposes the underlying dentine, compensatory shearing blades form (seen here as increased 2D blade length until ~18 years), resulting in the maintenance of 3D blade length. After 18 years, crest lengths plummet as the crown has been reduced to a shallow dentine basin surrounded by a low-relief enamel band.

slope appeared to have little functional significance because their disappearance by six years of age had little detrimental effect, as demographic data showed that sifakas live and reproduce many years beyond that age.

Because there is a well-known correlation in mammals between the length of shearing blades and food particle size reduction, regardless of exact cusp relief [65–67], we looked more closely at changes in crest lengths as tooth crowns lost relief and became relatively flatter. We ascertained that the relative 3D length of shearing blades on the mandibular molar is maintained for more than 10 years after teeth reach minimum relief values. GIS analysis revealed that this is accomplished by the formation of compensatory shearing blades as the enamel cover wears to reveal underlying areas of dentine surrounded by newly exposed enamel cutting edges. Thus, 2D crest length actually increased with wear up to a point (fig. 2b), and whereas the compensatory crests have low relief, their net effect is the maintenance of the overall 3D blade length. In both koalas and sifakas, 3D crest length eventually, and somewhat abruptly, plummets when the occlusal surface has been reduced to a shallow dentine bowl surrounded by a thin, low-relief enamel band and additional chewing strokes are required to process the same amount of food [68, 69]. We found that this ‘dental senescence’ occurs when sifaka females are approximately 18 years old. Our inference that the loss of compensatory shearing blades is an indication of dental senescence is supported by the analysis of low-magnification use wear [43, 63]. Wear scratches on the molar



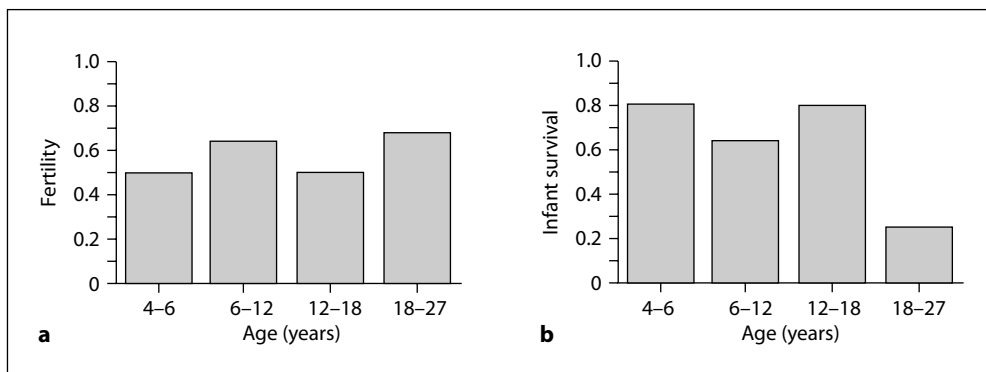


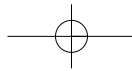
Fig. 3. Fertility and infant survival for four age classes of sifaka mothers. **a** Females of all age classes produce approximately one offspring every other year. **b** Old, dentally senescent mothers are less successful at rearing their offspring to adulthood than are younger mothers. Infant mortality due to infanticide (found only in infants of younger mothers) has been removed.

enamel decrease dramatically and in concert with plummeting blade lengths. Furthermore, observations of fecal samples of dentally prime versus dentally senescent females suggest that senescent females are less successful in reducing food particle size (ratios of >2 mm large seed fragments to >1 mm fragments: dentally senescent females -0.48 ; for dentally prime females -0.04 – 0.19).

Reproductive Senescence

Whereas dental topographic analysis suggests that sifaka females become dentally senescent at ~ 18 years of age, we demonstrated that fertility is undiminished in the same mature individuals (fig. 3a). Old females continued to be sexually active and continued to have infants until death. The mean interbirth interval was 1.5 years overall, but 1.2 years for older females, and this trend continues in the additional years analyzed for this study. At Ranomafana, these birth intervals for young and old mothers were not significantly different. In both young and old mothers the distribution of sexual behavior was seasonal and we estimated, by looking at birthdates of infants, that there was not any age difference in birth seasonality. Birth occurred in May–July regardless of mothers' age. In contrast to Old World monkeys, the frequency of proceptive behavior in lemurs was not more variable in younger versus older females.

Fertility remained high in dentally senescent mothers, but we found that those same mothers were less successful at rearing their offspring to adulthood (fig. 3b). The higher rate of infant mortality for dentally senescent mothers was not due to infanticide, which occurred only to the offspring of younger mothers. The data showed, however, that in years when rain was decreased during months of prime lactation, infants of dentally senescent mothers died before weaning. The cause may



have been the nursing mother's worn teeth, which could not shear leaves and extract moisture, nor nutrition, both essential for successful lactation.

The Question of Menopause

In the absence of hormonal data, menopause and true cessation of reproductive function in females cannot be confirmed [12]. However, the birth of infants is a good indicator that menopause has not occurred. In contrast to wild *Semnopithecus entellus* at Ramnagar where females were postmenopausal for up to five or more years prior to death, and at Jodpur where females were not reproducing in their last 3–5 years before death [39], these lemur females continued to give birth even after they were 30 years old [39].

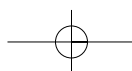
Social Disengagement and Behavioral Senescence

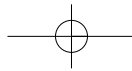
It has been suggested for anthropoids that aging females may become more socially disengaged [13, 19, 70–73]. In contrast to monkeys and apes, old lemur females would be predicted to be socially engaged, as females have priority of access to fruit trees, as well as resting sites [47, 74]. Thus, old females might be attractive as social partners. In order to examine this, we compared the number of night-time sleeping partners for old and young females.

We discovered that there were no significant differences between number of adult sleeping partners for the two young females: one slept with more than one individual 17 out of 21 nights; the other slept with more than one individual 21 out of 21 nights ($Z = -0.23$, $p = 0.902$). On the other hand, a Mann-Whitney U test indicated that there was a significant difference ($Z = -2.685$, $p = 0.007$) between the number of sleeping mates of young versus old adult females. This difference is largely due to the fact that the oldest female (aged 30 years) slept without any adult partners in 17 out of 21 nights. The 26-year-old female, when compared to the two younger females, showed no significant difference in sleeping partners ($Z = -1.019$, $p = 0.308$; $n = 63$, 21 old and 42 young). We anticipate that our sample size of extremely aged females will increase in future years enabling us to verify if this is indeed an age-related difference. That the oldest female typically slept alone suggests that at the end of life there may be the beginning of social disengagement, even while fertility remains high.

Conclusions and Future Directions

Senescence is infrequently observed in natural populations of large mammals [75] apparently because high rates of extrinsic mortality mean that few individuals live long enough to senesce. Primates may be unusually informative regarding senescence because they are a long-lived order, and among primates lemurs tend to live longer than anthropoids of similar body size. In this 20-year study of 17 lemur females we



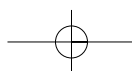


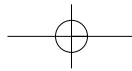
were able report that whereas Milne Edwards' sifakas showed signs of somatic (i.e. dental) senescence at 18 years, they showed no signs of menopause, even when they were over 30 years of age. Old females continued to be sexually active and continued to have infants until death. It should be noted that the mean interbirth interval was 1.5 years overall, but 1.2 years for older females. In other words, contrary to predictions from monkeys, old lemur females give birth more often than young lemur females. Furthermore, lemurs live as long or longer than most monkeys of comparable body mass, with a maximum lifespan of about 30–35 years for lemurs (at least 31 years are confirmed in captivity for 3 kg sifakas, 32–33 years for 2 kg brown lemurs and 3 kg black and white lemurs [Duke University Primate Center records; 15, 40]. Our results taken from a long-term study in the wild directly contrast with those for monkey females, who have been observed to spend up to 25% of their lives as nonreproductive [39]. In wild lemurs, we found no evidence for an extended post-reproductive lifespan. Of course, it remains unclear whether these conditions are the norm in all wild populations, but evidence from another long-term study of a smaller species of sifaka (*Propithecus verreauxi*) shows the same trend [41].

We suggest that the evolution of menopause is part of a continuum in primates. Menopause and the cessation of reproduction occur in the first half of the maximum lifespan for humans [27], and cessation of reproduction may occur in the last quarter of a monkey's lifespan [18, 39]. Lemurs, on the other hand, do not show any slowdown in producing offspring until death, but offspring survival is diminished in the oldest females. This pattern may have evolved to produce the maximum number of offspring in the unpredictable environment of Madagascar, as in years with sufficient rainfall in the dry season, infants, even of older mothers do survive [43, 57, 76]. To the extent that our lemur results reflect the basal primate mode of senescence, the evolution of menopause may have its origin in a long lifespan that compromises females' ability to buffer their reproductive success against environmental fluctuations. Data on more populations of lemurs, including tracking reproductive hormones, will help to understand this prosimian mode of reproductive senescence.

Acknowledgements

We express our sincere gratitude to Sylvia Atsalis, Sue Margulis and Patrick Hof for inviting us to participate in the aging volume. We acknowledge the government of Madagascar and the CAFF/CORE oversight committee for authorization to do work in Madagascar. We appreciate the help with logistics and infrastructure from MICET, Centre ValBio and ANGAP. Thanks to our research assistants who have helped collect these data including Georges René Randrianirina, Remi Rakotosoa, the late Georges Rakotonirina, Raymond Ratsimbazafy, Laurent Randrianasolo, Telo Albert. Thanks to Dr. Jeff Wyatt for his veterinary expertise, Toni Lyn Morelli and Summer Arrigo-Nelson for their assistance with capture and observations, Gina Semprebbon for dental microwear analysis, and Laurie Godfrey for her expertise on life history in lemurs. Particular thanks to the many donors, which have supported the work: National Science Foundation, USA, Wenner-Gren Foundation, Norman and Lucile Packard Foundation, Earthwatch Institute, Stony Brook

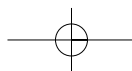




University Study Abroad Program and the University of Helsinki Center for excellence grant. All work reported here was approved by IACUC Stony Brook University and complied with the laws of Madagascar.

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