Available online at www.sciencedirect.com
SCIENCE DIRECT®

ELSEVIER

JHE

Journal of Human Evolution 46 (2004) 623–631

News and Views

Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids

Frank P. Cuozzo[a]*, Michelle L. Sauther[b]

[a] *Department of Anthropology, Northern Illinois University, DeKalb, IL 60115, USA*
[b] *Department of Anthropology, University of Colorado, Campus Box 233, Boulder, CO 80309-0233, USA*

Received 8 December 2003; accepted 27 February 2004

Keywords: Lemurs; Dental pathology; Hominid paleobiology; Life history; Beza Mahafaly

Introduction

The degree of antemortem tooth loss seen in wild nonhuman primates is central to the ongoing debate concerning conspecific care in fossil hominids (see Holden, 2003). Lebel and Trinkaus (2002) argued that the extreme (≥81.8%) antemortem tooth loss seen in Aubesier 11, a partial hominid mandible from the middle Pleistocene (Lebel et al., 2001), exceeds that of known samples of living nonhuman primates. Their argument follows that, because of its severely impaired masticatory system, this individual would have required some form of social assistance to survive (Lebel et al., 2001; Lebel and Trinkaus, 2002). DeGusta (2002, 2003) refuted this, arguing that the degree of tooth loss in archaic humans does not exceed that of wild nonhuman primates. Of interest, both Lebel and Trinkaus (2002) and DeGusta (2003) cited data on dental health in the population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Special Reserve, Madagascar (Sauther et al., 2002) in their arguments. As noted by DeGusta (2003), Lebel and Trinkaus (2002) were incorrect in their characterization of the data presented by Sauther et al. (2002), arguing that "wild-trapped individuals with extensively worn teeth disappear shortly after observation" (Lebel and Trinkaus, 2002: 672). Rather, Sauther et al. (2002) reported the long-term survival (several years) of two ring-tailed lemurs with pronounced dental impairment. However, the data on tooth loss and individual survival presented by Sauther et al. (2002) were descriptive, rather than quantitative, and illustrate the need for comprehensive data on dental health and tooth loss in wild nonhuman primates.

When considering hominid paleobiology in a comparative context, the choice of an appropriate analogue is important. Lebel and Trinkaus (2002) argued that the most appropriate direct comparison for understanding hominid paleobiology and inferring conspecific care in middle Pleistocene hominids is other archaic human populations, as the social systems and technology associated with modern human groups limit their relevance. They also noted the significance of large-bodied, wild

* Corresponding author. Tel.: +1-815-753-0744; fax: +1-815-753-7027
E-mail addresses: fcuozzo@niu.edu (F.P. Cuozzo), sauther@stripe.colorado.edu (M.L. Sauther).

0047-2484/04/$ - see front matter
doi:10.1016/j.jhevol.2004.02.004

nonhuman primates in a comparative context, and acknowledged the relevance of data from a wide range of taxa (e.g., ring-tailed lemurs). Previous data on antemortem tooth loss in nonhuman primates primarily come from skeletal samples. In addition, these data most often represent haplorhine primates (e.g., Schultz, 1935; Bramblett, 1969; Hershkovitz, 1970; Smith et al., 1977; Kilgore, 1989; Lovell, 1990; Miles and Grigson, 1990; Stoner, 1995; DeGusta and Milton, 1998). While some may question the significance of data on ring-tailed lemurs for discussions of hominid paleobiology, among strepsirrhine primates, *Lemur catta* provides the most appropriate point of comparison. Given their semi-terrestrial locomotion, diurnality, complex group structure, and mixed diet, ring-tailed lemurs differ considerably from more specialized strepsirrhines, and are comparable in a number of attributes to many haplorhine primates (e.g., Sussman, 1992; Sauther et al., 1999). The analysis of fossil hominids in a broad comparative context is an important perspective (see Conroy, 2002). Therefore, data from a wide range of nonhuman primates are imperative for understanding hominid paleobiology within a broad primate (and mammalian) context.

Our purpose in this report is to present recently collected data on antemortem tooth loss in the population of ring-tailed lemurs at Beza Mahafaly Special Reserve. These data allow us to address the following questions in the debate surrounding hominid conspecific care:

1. Does the degree of antemortem tooth loss in fossil hominids exceed that in a living, wild nonhuman primate population?
2. Do nonhuman primates that subsist partly on tough foods survive despite tooth loss?
3. Do nonhuman primates survive with impaired masticatory systems under natural conditions (i.e., without human intervention)?

Materials and methods

The ring-tailed lemur population at Beza Mahafaly Special Reserve, Madagascar has been the focus of ongoing, long-term study (e.g., Sauther, 1989, 1991; Sussman, 1991, 1992; Gould et al., 1999, 2003; Sauther et al., 1999, 2001, 2002; Yamashita, 2003). As part of this research, we collected data on dental health (including information on tooth loss) from a sample of 71 individuals in 2003. The lemurs in our sample come from “camp groups” (those troops that have access to and utilize [primarily unintentional] human-derived resources [e.g., water, food waste, crops]) and “reserve groups” (those troops that subsist on natural diets, both in the protected Beza Mahafaly Reserve, and in more degraded habitat in close proximity to the reserve). Of the lemurs we studied, 19 come from “camp groups” with the remainder (52) coming from “reserve groups.” We also evaluated the overall health status of these individuals, based on (but not limited to) the presence or absence of external wounds, traumatic injuries, infections, and ectoparasites.

Of the 71 individuals captured and studied, 65 exhibited full adult dentitions, and the data on tooth loss presented here are based on these individuals. Teeth were recorded as missing if either no trace of the tooth was present (i.e., no evidence of roots), or if the tooth was completely worn down to (or below) the gumline with only individual roots remaining (see Figs. 1 and 2). We recognize that our method of scoring tooth loss differs from that used for skeletal and/or fossil specimens, as bone remodeling and other alveolar changes are not visible in living animals. However, we feel that our data are comparable to those of previous studies, as the focus remains the documentation of impaired dental function. We also examined 16 crania/partial skulls in the Beza Mahafaly Osteology Collection (BMOC) for indications of antemortem tooth loss, in order to supplement our data on living lemurs.

Results

Table 1 presents data on antemortem tooth loss in living ring-tailed lemurs at Beza Mahafaly compared with late archaic humans (Lebel and Trinkaus, 2002) and extant large-bodied hominoids (Lovell, 1990). In the ring-tailed lemur sample, 27.7% of the individuals exhibit at least

Fig. 1. Maxillary tooth loss in a living ring-tailed lemur (Yellow 195). Note the areas of tooth loss, with only roots remaining (white arrows).

some tooth loss. This compares with 29.2% for gorillas, 18.2% for late archaic *Homo*, 16.7% in chimpanzees, and 5.9% in orangutans. Instances of more severe tooth loss are greater in ring-tailed lemurs: 10.8% of the individuals in our sample exhibit greater than 30% tooth loss, compared with 6.6% for chimpanzees, 4.6% for late archaic humans and gorillas, and 0% for orangutans. In both ring-tailed lemurs and late archaic humans, 4.6% of individuals exhibit the most extreme category of tooth loss (>50%), compared with 3.3% for chimpanzees, and 0% for both gorillas and orangutans.

In terms of the skeletal data, three of the 16 crania/partial skulls in this collection display obvious antemortem tooth loss, with two individuals having each lost at least one upper molar (based on remodeling of the alveoli). The remaining specimen exhibits an antemortem loss of at least 28% (5 of 18) of the maxillary teeth (no mandible was

Fig. 2. Mandibular tooth loss in a living ring-tailed lemur (Orange 170). Note the areas of tooth loss, with only roots remaining (black arrows).

available for this specimen). Unequivocal bone remodeling in the alveolar region has occurred in this individual (Fig. 3), and our observations indicate the antemortem loss of at least left M^{1-2} and right P^4 through M^2. This is significant, in that the excessive bone remodeling in this specimen indicates a prolonged period of survival, despite tooth loss and a severely impaired masticatory system.

Discussion

In his study of dental pathology and tooth loss in primates, Schultz (1935) noted that impaired dental function resulting from tooth wear, disease, and antemortem tooth loss was more common in humans and apes than in other primates (he did not include data on strepsirrhines). Lebel and Trinkaus (2002) argued that 25% or greater antemortem tooth loss (like the $\geq$81.8% seen in Aubesier 11) is rare among wild primates. These patterns are not supported by our ring-tailed lemur sample, in which the overall percentage of individuals with at least some tooth loss (except *Gorilla*), as well as more pronounced loss (>30%), is higher than that for large-bodied hominoids (Lovell, 1990) and late archaic humans (Lebel and Trinkaus, 2002). In addition, 14% of the individuals in our living sample exhibit at least a 25% tooth loss.

As Schultz (1935) noted, the life history of primates is an important variable when considering dental pathology and tooth loss. One possible

Table 1
Percentage of antemortem tooth loss in living ring-tailed lemurs at Beza Mahafaly Special Reserve compared with late archaic humans and extant large-bodied hominoids

% Antemortem tooth loss[a]	*Lemur catta* (%)	Late archaic *Homo*[b] (%)	*Pan troglodytes*[c] (%)	*Gorilla gorilla*[c] (%)	*Pongo pygmaeus*[c] (%)
0	72.3	81.8	83.3	70.8	94.1
1–10	13.8	4.5	3.3	18.5	5.9
11–20	0	4.5	3.3	3.1	0
21–30	3.1	4.5	3.3	3.1	0
31–40	3.1	0	0	4.6	0
41–50	3.1	0	3.3	0	0
51–60	3.1	2.3	3.3	0	0
61–100	1.5	2.3	0	0	0
n	65	44	30	65	34

[a]% Antemortem tooth loss represents the number of teeth missing in an individual divided by the total of number of tooth positions and multiplied by 100.
[b]Percentages from Lebel and Trinkaus (2002).
[c]Percentages calculated from data in Lovell (1990).

cause for the high percentage of tooth loss in our sample is the faster life history schedule of *Lemur catta* when compared to large-bodied hominoids, including hominids (e.g., Harvey and Clutton-Brock, 1985; Harvey et al., 1987). Even among lemurids, *L. catta* exhibits an accelerated dental development schedule (Godfrey et al., 2004), with an earlier eruption of M1 than either *Eulemur* or *Varecia* (e.g., Eaglen, 1985). Despite not having all adult teeth in place, we observed that subadult ring-tailed lemurs begin to display noticeable wear on their adult mandibular first molars. Based on our analysis of living and skeletal specimens at Beza Mahafaly, first molars (both maxillary and mandibular) are usually the first adult teeth to exhibit wear, and are often the first teeth lost. In our sample of living individuals, 16 of the 18 with at least some tooth loss, and seven of the eight individuals missing only one or two teeth, are missing a first molar. In addition, among those individuals that retain a first molar, many show excessive wear relative to other teeth. Tooth wear results from a complex interaction of variables, including diet, occlusal form, and enamel quantity. Early eruption of M1, combined with the use of tough foods (see below), may therefore contribute to the higher overall percentage of individuals in our sample with at least some tooth loss, compared with most large-bodied hominoids.

A key issue for the question of conspecific care in fossil hominids is whether nonhuman primates can survive with tooth loss under "natural" conditions (without access to human-derived resources). Both Lebel and Trinkaus (2002) and DeGusta (2002) suggested caution when using Kilgore's (Kilgore, 1989) data on tooth loss in the chimpanzees from Gombe National Park, as human provisioning of this population calls into question the use of these data in a comparative context. In our sample, the majority (72%) of the 18 individuals that exhibit antemortem tooth loss come from one of the "reserve groups," with only five (28%) coming from a "camp group." In terms of more severe tooth loss, five of the seven individuals with a greater than 30% tooth loss, and three of the four with at least a 50% tooth loss, come from "reserve groups." These data confirm that under "natural" conditions, pronounced antemortem tooth loss is a common occurrence in nonhuman primate populations, as recognized years ago by Schultz (1935).

Also of interest in this context is the diet of *Lemur catta*. Lebel and Trinkaus (2002) argued that, unlike archaic humans, nonhuman primates

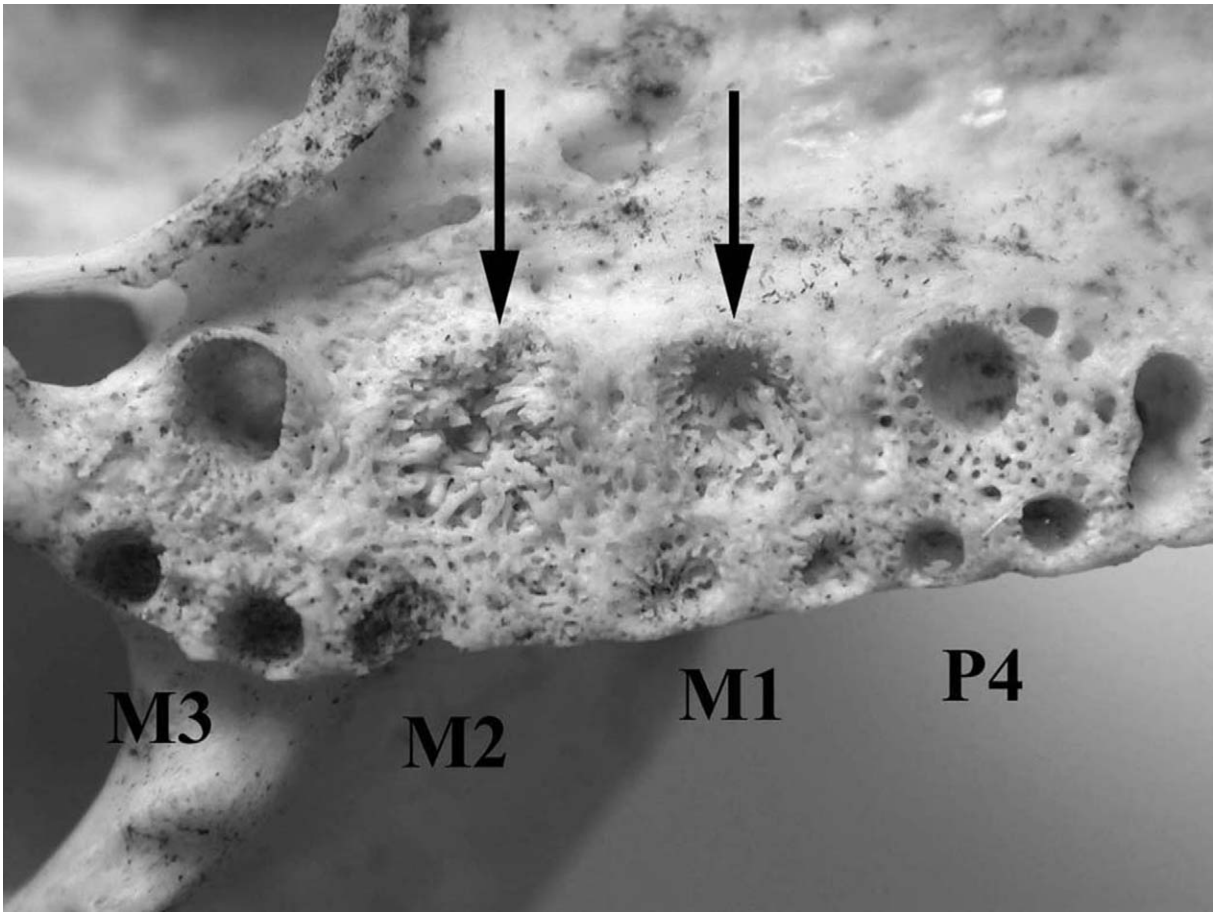

Fig. 3. Antemortem tooth loss in an uncatalogued *Lemur catta* specimen in the Beza Mahafaly Osteology Collection (BMOC). This image illustrates the left alveolar region of the maxilla, with the arrows denoting the nearly obliterated lingual alveoli of M^{1-2}.

subsist, at least in part, on the soft portions of plants. Subsequently, they argued that the possible survival of nonhuman primates with impaired dental function differs from that of fossil hominids. Ring-tailed lemurs utilize a variety of foods (e.g., Sauther et al., 1999; Yamashita, 2003), with the tamarind tree (*Tamarindus indica*) being a keystone food source (Jolly, 1966; Sauther, 1998; Sauther et al., 2002). Tamarind pods (a common food item) have a tough outer casing that requires high magnitude forces to crack in order to access the encased fruit (Yamashita, 2003). These pods are often initially processed by the postcanine teeth (Sauther et al., 2002; Yamashita, 2003). As this food source is integral for ring-tailed lemurs, and as postcanine teeth are usually the first lost, the survival of individuals with pronounced tooth loss suggests the ability to process this tough food despite masticatory impairment—without the aide of the stone tools available to archaic hominids.

Previously, Sauther et al. (2002) reported the three-year survival of a nearly edentulous individual in the Beza Mahafaly population. This individual was in excellent health in 1987, and survived through the 1990 census. As seen in Table 2, two of the individuals with at least a 50% antemortem tooth loss in the current sample are in overall good health (Yellow 195, Orange 170), with one each rated as fair (Blue 132) and poor (Hot Pink 188). Of interest, the latter two individuals are from

Table 2
Detailed information on dental pathology for living ring-tailed lemurs at Beza Mahafaly Special Reserve with at least a 50% antemortem tooth loss

Individual	Troop	Camp/Reserve	%Tooth loss	Missing teeth	Other dental damage	Overall health
195	Yellow	Reserve	50%	LP^{3-4}, LM^{1}, LP_{3-4}, LM_{1-3}, RI^{1}, RP^{2-4}, RM^{1}, RP_{3-4}, RM_{1-3}	All teeth in toothcomb broken at ends	Good
188	Hot Pink	Reserve (degraded)	56%	LP^{3-4}, LM^{1-2}, LI_{1}, LP_{3-4}, LM_{1-2}, RP^{2-4}, RM^{1-2}, RI_{1}, RP_{3-4}, RM_{1-3}	Remaining teeth with heavy wear	Poor
132	Blue	Reserve (degraded)	56%	LP^{3-4}, LM^{1-2}, LI^{1-2}, LM_{1}, LP_{3-4}, RP^{3-4}, RM^{1-2}, RI^{1-2}, RM_{1}, RP_{3-4}, RI_{1-2} or RI_{1} and LI_{1}	Both canines in toothcomb broken, remaining teeth with severe wear	Fair
170	Orange	Camp	61%	LP^{2-4}, LM^{1-2}, LI_{1-2}, LP_{3-4},LM_{1-3}, RP^{3-4}, RM^{1-2}, RI_{1}, RP_{3-4}, RM_{1-3}	Both canines in toothcomb broken, remaining teeth with heavy wear	Good

degraded habitat: Yellow 195 is from the protected reserve and Orange 170 is from a camp group. In fact, of the 65 adults studied, only nine were rated as fair or poor, and of these nine, only three (each from degraded habitat) displayed significant (>10%) tooth loss. These data suggest that habitat and resource availability, rather than tooth loss and the impaired ability to process food, are largely responsible for individual health status.

Conclusions

Our data provide information on the frequency of antemortem tooth loss in a wild nonhuman primate population, including its correlation with health, habitat, resource use, and individual survival. Previous studies have also described antemortem tooth loss in nonhuman primates, but our data confirm that, under natural conditions (i.e., without access to human-derived resources), the survival of animals with impaired masticatory systems is not a rare occurrence. Our data, combined with those of previous studies, call into question the validity of inferring conspecific care in fossil hominids based on the presence of even severe antemortem tooth loss in hominid specimens. Direct comparisons between fossil hominids and any single extant nonhuman primate taxon are inappropriate. Therefore, the presence of antemortem tooth loss in a broad range of extant primates provides an important framework for interpreting hominid paleobiology (e.g., DeGusta, 2002). Given their food processing technology and a trend towards dental reduction over time (e.g., Hillson, 1996), the survival of archaic humans with extreme tooth loss seems less remarkable in light of our data. Although some previous studies indicate a low frequency of antemortem tooth loss in wild nonhuman primates (e.g., Stoner, 1995), our data clearly demonstrate that a number of nonhuman primates live under natural conditions with pronounced tooth loss and severe masticatory impairment for some time.

Acknowledgements

We thank Enafa Efitroaromy, Edidy Ellis, Krista Fish, Mandala Hunter, Heather Culbertson, and David Miller for their assistance with data collection at Beza Mahafaly during the 2003 field season. We also thank Robert W. Sussman, Ingrid Porton, Randy Junge, Joel Ratsirarson, and Jo Ajimy for their strong support and facilitation of our project. Our appreciation also goes to the Département des Eaux et Forêts, Ecole Superieur des Sciences Agronomiques, Université d'Antananarivo for allowing us to continue our research at Beza Mahafaly. We thank all who have contributed to the organization and maintenance of the Beza Mahafaly Osteology Collection. David Degusta, Debbie Guatelli-Steinberg, and Gary Schwartz provided many helpful comments on an earlier version of our paper. We also thank David DeGusta for his discussion of Lovell's, (1990) hominoid tooth loss data. We thank Bill Kimbel and three anonymous referees for their suggestions. Funding for this study came from the Lindbergh Fund, The Saint Louis Zoo, and the University of Colorado, Boulder.

References

Bramblett, C.A., 1969. Non-metric skeletal age changes in the Darajani baboon. Am. J. Phys. Anthrop. 30, 161–172.

Conroy, G.C., 2002. Speciosity in the early *Homo* lineage: too many, too few, or just about right? J. Hum. Evol. 43, 759–766.

DeGusta, D., 2002. Comparative skeletal pathology and the case for conspecific care in middle Pleistocene hominids. J. Archaeol. Sci. 29, 1435–1438.

DeGusta, D., 2003. Aubesier 11 is not evidence of Neanderthal conspecific care. J. Hum. Evol. 45, 91–94.

DeGusta, D., Milton, K., 1998. Skeletal pathologies in a population of *Alouatta palliata*: behavioral, ecological, and evolutionary implications. Int. J. Primatol. 19, 615–650.

Eaglen, R.H., 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. Am. J. Phys. Anthrop. 66, 307–315.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T., 2004. Ontogenetic correlates of diet in Malagasy lemurs. Am. J. Phys. Anthrop. 123, 250–276.

Gould, L., Sussman, R.W., Sauther, M.L., 1999. Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. Int. J. Primatol. 20, 69–84.

Gould, L., Sussman, R.W., Sauther, M.L., 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly, Madagascar: a 15-year perspective. Am. J. Phys. Anthrop. 120, 182–194.

Harvey, P.H., Clutton-Brock, T.H., 1985. Life history variation in primates. Evolution 39, 559–581.

Harvey, P.H., Martin, R.D., Clutton-Brock, T.H., 1987. Life histories in comparative perspective. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhasker, T.T. (Eds.), Primate Societies. University of Chicago Press, Chicago, pp. 181–196.

Hershkovitz, P., 1970. Dental and periodontal diseases and abnormalities in wild-caught marmosets (Primates—Callithricidae). Am. J. phys. Anthrop. 32, 377–394.

Hillson, S., 1996. Dental Anthropology. Cambridge University Press, Cambridge.

Holden, C., 2003. Neandertals not caring? Science 301, 1319.

Jolly, A., 1966. Lemur Behavior. University of Chicago Press, Chicago.

Kilgore, L., 1989. Dental pathologies in ten free-ranging chimpanzees from Gombe National Park, Tanzania. Am. J. Phys. Anthrop. 80, 219–227.

Lebel, S., Trinkaus, E., Faure, M., Fernandez, P., Guérin, C., Richter, D., Mercier, N., Valladas, H., Wagner, G.A., 2001. Comparative morphology and paleobiology of middle Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France. Proc. Natl. Acad. Sci. 98, 11097–11102.

Lebel, S., Trinkaus, E., 2002. Middle Pleistocene human remains from the Bau de l'Aubesier. J. Hum. Evol. 43, 659–685.

Lovell, N.C., 1990. Patterns of Injury and Illness in Great Apes: A Skeletal Analysis. Smithsonian Institution Press, Washington, DC.

Miles, A.E.W., Grigson, C., 1990. Colyer's Variations and Diseases of the Teeth of Animals. Cambridge University Press, Cambridge.

Sauther, M.L., 1989. Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Int. J. Primatol. 10, 595–606.

Sauther, M.L., 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Am. J. Phys. Anthrop. 84, 463–477.

Sauther, M.L., 1998. The interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. Folia primatol. 69(Suppl.), 309–320.

Sauther, M.L., Cuozzo, F.P., Sussman, R.W., 2001. Analysis of dentition of a living, wild population of ring-tailed lemurs (*Lemur catta*) from Beza Mahafaly, Madagascar. Am. J. Phys. Anthrop. 114, 215–223.

Sauther, M.L., Sussman, R.W., Cuozzo, F., 2002. Dental and general health in a population of wild ring-tailed lemurs: a life history approach. Am. J. Phys. Anthrop. 117, 122–132.

Sauther, M.L., Sussman, R.W., Gould, L., 1999. The socio-ecology of the ring-tailed lemur: thirty-five years of research. Evol. Anthrop. 8, 120–132.

Schultz, A.H., 1935. Eruption and decay of the permanent teeth in primates. Am. J. Phys. Anthrop. 19, 489–588.

Smith, J.D., Genoways, H.H., Jones, J.K., 1977. Cranial and dental anomalies in three species of platyrrhine monkeys from Nicaragua. Folia primatol. 28, 1–42.

Stoner, K.E., 1995. Dental pathology in *Pongo satyrus borneensis*. Am. J. Phys. Anthrop. 98, 307–321.

Sussman, R.W., 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. Am. J. Phys. Anthrop. 84, 43–58.

Sussman, R.W., 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). Int. J. Primatol. 13, 395–413.

Yamashita, N., 2003. Food procurement and tooth use in two sympatric lemur species. Am. J. Phys. Anthrop. 121, 125–133.