

Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history

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Abstract

The ring-tailed lemurs at Beza Mahafaly Special Reserve, Madagascar, exhibit a high frequency of severe wear and antemortem tooth loss. As part of a long-term study, we collected dental data on 83 living adult ring-tailed lemurs during 2003 and 2004. Among these individuals, 192 teeth were scored as absent. The most frequently missing tooth position is M1 (24%). As M1 is the first tooth to erupt, its high frequency of absence (primarily a result of wear) is not remarkable. However, the remaining pattern of tooth loss does not correlate with the sequence of eruption. We suggest that this pattern is a function of 1) feeding ecology, as hard, tough tamarind fruit is a key fallback food of ring-tailed lemurs living in gallery forests; 2) food processing, as tamarind fruit is primarily processed in the P3–M1 region of the mouth; and 3) tooth structure, as ring-tailed lemurs possess thin dental enamel. The incongruity between thin enamel and use of a hard, tough fallback food suggests that ring-tailed lemurs living in riverine gallery forests may rely on resources not used in the past. When comparing dental health in the same individuals ($n = 50$) between 2003 and 2004, we found that individual tooth loss can show a rapid increase over the span of one year, increasing by as much as 20%. Despite this rapid loss, individuals are able to survive, sometimes benefiting from unintentional assistance from conspecifics, from which partially processed tamarind fruit is obtained. Although less frequent in this population, these longitudinal data also illustrate that ring-tailed lemurs lose teeth due to damage and disease, similar to other nonhuman primates. The relationship between tooth loss, feeding ecology, dental structure, and individual life history in this population has implications for interpreting behavior based on tooth loss in the hominid fossil record.

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Introduction

Mammalian teeth document an individual's ontogeny (e.g., Maas and Dumont, 1999; Schwartz and Dean, 2000; Godfrey et al., 2005; Schwartz et al., 2005), including periods of developmental stress (e.g., Guatelli-Steinberg, 2001). In addition, mammalian teeth (and their accompanying alveoli) record an individual's life experience, seen for example in patterns of tooth wear, disease, and tooth loss. Thus, teeth provide

evidence of an individual's life story (e.g., Morbeck, 1997). Although dental enamel is a very hard substance, noticeable and often dramatic tooth wear occurs across the mammalian radiation (e.g., Hillson, 1986, 2005; Kaifu et al., 2003; Lucas, 2004). Primates are no exception (e.g., Schultz, 1935; Smith et al., 1977; Janis and Fortelius, 1988; Kilgore, 1989; Teaford, 2000; King et al., 2005).

Tooth wear results from a complex interaction of variables, including behavior (e.g., culture among humans), diet, food properties, mastication and food processing, tooth morphology, and enamel quantity (e.g., Molnar, 1971; Smith et al., 1977; Smith, 1984; Hillson, 1996; Gandara and Truelove, 1999; Maas and Dumont, 1999; Verrett, 2001; Kaifu et al., 2003; Lucas, 2004; Lussi et al., 2004). In addition, tooth

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wear is, in general, an age-related phenomenon (Hillson, 1996), with older individuals exhibiting more wear. In some cases, tooth wear becomes so advanced that the tooth crowns are lost, with these teeth (often including their associated roots) becoming completely absent during the life of the individual (i.e., antemortem tooth loss). Antemortem tooth loss also results from periodontal disease and/or other pathologies (e.g., Schultz, 1935; Smith et al., 1977; Hillson, 1986; Lovell, 1990; Stoner, 1995). Data on patterns of dental health in wild nonhuman primates, including information on tooth loss, come primarily from skeletal samples, and most often represent haplorhine primates (e.g., Schultz, 1935; Bramblett, 1969; Smith et al., 1977; Kilgore, 1989; Miles and Grigson, 1990; Lovell, 1990; Philips-Conroy et al., 1993; Stoner, 1995; DeGusta and Milton, 1998). In addition, data from single primate populations for which behavioral and/or ecological data are available are quite rare (e.g., Kilgore, 1989; Philips-Conroy et al., 1993). Only recently have data on dental health and tooth wear from single populations of living strepsirrhines become available (e.g., Sauter et al., 2002; Cuzzo and Sauter, 2004; Cuzzo et al., 2004a,b; King et al., 2005).

The ring-tailed lemurs (*Lemur catta*) of Beza Mahafaly Special Reserve, southwestern Madagascar (23° 30' S latitude, 44° 40' E longitude), are notable for their high frequency of severe wear and tooth loss (Fig. 1) when compared to large-bodied hominoids (Cuzzo and Sauter, 2004). This is especially true when compared to thick-enameled orangutans (Cuzzo and Sauter, 2004), which generally exhibit fewer missing teeth (Lovell, 1990; Stoner, 1995) and later occurring

wear than do thin-enameled chimpanzees and gorillas (Dean et al., 1992). Enamel thickness has long been recognized as an important phylogenetic and/or adaptive variable in humans and other primates (e.g., Molnar and Gantt, 1977; Kay, 1981, 1985; Dumont, 1995; Schwartz and Dean, 2000; Teaford and Ungar, 2000; Ungar, 2002; Smith et al., 2003; Hlusko et al., 2004; Grine, 2004; Godfrey et al., 2005), and enamel thickness generally shows a strong correlation with diet (e.g., Kay, 1981, 1985; Dumont, 1995; Shellis et al., 1998; Maas and Dumont, 1999; Hlusko, 2004). Although thick-enameled primates usually subsist on hard and/or tough foods (e.g., Kay, 1981, 1985; Dumont, 1995; Shellis et al., 1998; Teaford and Ungar, 2000), the relationship between diet and enamel thickness is not perfect (e.g., Maas and Dumont, 1999; Teaford and Ungar, 2000; Martin et al., 2003; Liu and Zheng, 2005). However, the ability to mechanically process specific foods, especially those fallback foods (i.e., foods relied upon during periods of nutritional stress) that allow survival and therefore provide a selective advantage, likely play a key role in the evolution of primate enamel thickness (e.g., Lambert et al., 2004). Also, it appears that primate enamel thickness may rapidly reflect dietary shifts, thereby being subject to homoplasy, which reduces its phylogenetic value (Hlusko, 2004). Ring-tailed lemurs living in the riverine gallery forests of southern Madagascar, despite possessing thin enamel [among the most thin-enameled of all extant primates for which data are available (e.g., Shellis et al., 1998; Martin et al., 2003; Godfrey et al., 2005; see Table 1)], rely on hard, tough foods [i.e., products of the tamarind tree, *Tamarindus indica* (e.g., Sauter, 1992, 1998; Yamashita, 2000, 2002, 2003, in preparation; Cuzzo and Sauter, 2004, 2006; Simmen et al., 2006)], yet are able to successfully survive for a number of years with severe dental wear and tooth loss (Sauter et al., 2002; Cuzzo and Sauter, 2004).

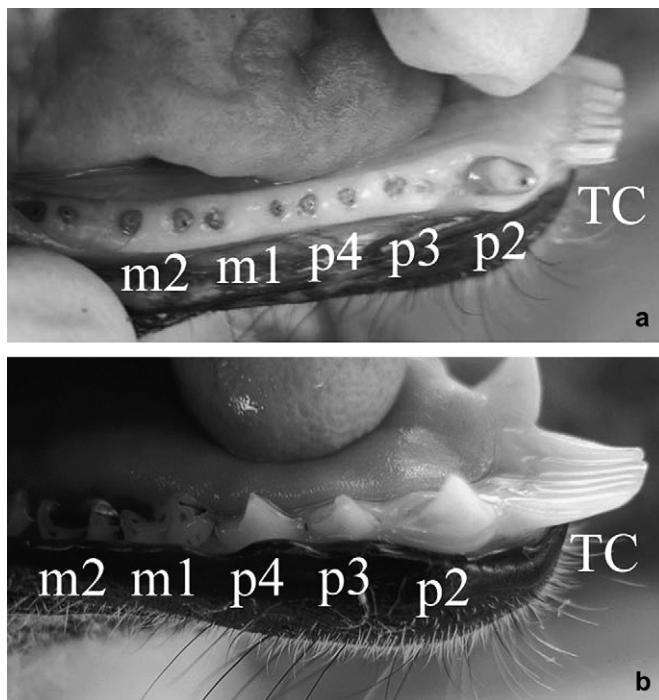


Fig. 1. Tooth loss in a living ring-tailed lemur. (a) Absence of *Lemur catta* mandibular teeth, with only worn roots remaining (Yellow 195). Note the worn toothcomb (=TC). (b) Normal (limited wear) mandibular teeth in *Lemur catta* (Teal 205). Note the unworn toothcomb (=TC).

Table 1

Relative enamel thickness (R.E.T.) of ring-tailed lemurs compared with other primates

Taxon ^a	Mean R.E.T. ^{a,b}
<i>Varecia variegata</i> †	5.7
<i>Lemur catta</i> †	7.3
<i>Gorilla gorilla</i>	10.0
<i>Pan troglodytes</i>	10.1
<i>Propithecus verreauxi</i> †	10.7
<i>Hylobates lar</i>	11.0
<i>Paleopropithecus ingens</i> † (extinct)	11.3
<i>Propithecus diadema</i> †	13.0
<i>Hadropithecus stenognathus</i> † (extinct)	14.4
<i>Papio cynocephalus</i>	15.4
<i>Theropithecus gelada</i>	15.6
<i>Pongo pygmaeus</i>	15.9
<i>Cebus apella</i>	19.2
<i>Daubentonia madagascariensis</i> †	21.7
<i>Homo sapiens</i>	22.4
<i>Archaeolemur majori</i> † (extinct)	28.3

† = Malagasy strepsirrhine taxa.

^a Data adapted from Godfrey et al. (2005).

^b See Schwartz et al. (2003) and Godfrey et al. (2005) for method of calculating relative enamel thickness.

In addition to dental microstructure, there is a large body of data demonstrating a relationship between tooth morphology and diet in primates and other mammals (e.g., Kay, 1975, 1978; Seligsohn, 1977; Lucas, 1979, 2004; Kinzey and Norconck, 1990; Strait, 1993; Yamashita, 1998; Ungar, 1998; Ungar and M'Kirera, 2003; see review in Cuozzo and Yamashita, 2006). However, in primates with a more generalized diet (e.g., *Lemur catta*), the relationship between tooth morphology and diet becomes less distinct (e.g., Cuozzo and Yamashita, 2006). Included within this work are analyses of the relationship between tooth morphology and the mechanical properties of food (e.g., Strait, 1997; Lucas, 2004). Although a number of more recent studies have investigated food properties in the field (e.g., Kinzey and Norconck, 1990; Lucas et al., 1991, 1995; Wright, 2005), to date there have been few studies of the physical properties of foods consumed by lemurs (Strait and Overdorff, 1996; see review in Cuozzo and Yamashita, 2006). Among the lemurs for which data on food properties are available are the ring-tailed lemurs and sympatric Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly (e.g., Yamashita, 1998, 2000, 2002, 2003).

The ring-tailed lemurs at Beza Mahafaly have been the focus of long-term research (e.g., Ratsirarson, 1985; Sauter, 1989, 1991, 1992, 1998; Sussman, 1991, 1992; Gould, 1996, 1997; Yamashita, 1998, 2000, 2002, 2003; Gould et al., 1999, 2003; Sauter et al., 1999, 2001, 2002, 2004, 2006; Cuozzo and Sauter, 2004, 2006; Cuozzo et al., 2004a,b; for detailed descriptions of the reserve at Beza Mahafaly, see Sussman and Rakotozafy, 1994; Sauter et al., 1999; Gould et al., 1999, 2003; Ratsirarson, 2003). Among primates, this population is rare in that detailed, longitudinal dental data (including sets of dental casts) are available for the population, as well as for specific individuals, some of which are of known age (for additional examples, see Dennis et al., 2004; King et al., 2005; and Lawler et al., 2005). In addition, detailed information on feeding ecology, behavior, habitat, and patterns of general health are also known, both for the population as a whole, and for specific individuals. Therefore, information on individual life stories is available for many members of the population (e.g., Sauter et al., 2002, in preparation; Cuozzo and Sauter, 2004).

Research questions

Previously, we described patterns of tooth damage, dental pathology, and tooth loss in the ring-tailed lemur population at Beza Mahafaly (e.g., Sauter et al., 2002; Cuozzo and Sauter, 2004). However, these data represent single points in time, as they were based on information collected during individual field seasons. As such, our previous discussions emphasized population characteristics, and usually did not address questions of longitudinal change among individuals. Here we discuss in detail the probable causes of severe wear and tooth loss in the Beza Mahafaly ring-tailed lemur population, and relate these patterns to feeding ecology, tooth structure, and individual life history, based on data collected across two field seasons (supplemented with data from earlier work

on this population). These data include information on changes in dental health in individual lemurs, preliminary behavioral observations related to surviving tooth loss, and a comparison of tooth loss with sympatric *P. verreauxi*. Thus, as part of our long-term research on this population of ring-tailed lemurs, we present new information on patterns of tooth wear and antemortem tooth loss and address the following questions:

- 1) Does the frequency of tooth loss correspond to the placement of food during mastication?
- 2) Do tooth loss frequencies correspond to the sequence of dental eruption?
- 3) Does tooth loss increase in the same individuals over the span of one year?
- 4) How do patterns of severe wear and tooth loss in ring-tailed lemurs compare with sympatric Verreaux's sifaka?
- 5) How are ring-tailed lemurs able to survive despite severe dental impairment and a diet dependent on hard, tough foods?

As we include information on tooth loss and behavior, we also expand on our previous discussion (Cuozzo and Sauter, 2004) of behavior in the hominid fossil record based on patterns of antemortem tooth loss in extant primates.

Materials and methods

During June and July of 2003 and 2004, as part of our comprehensive research project, we collected dental data from sedated ring-tailed lemurs at the Beza Mahafaly Special Reserve. The 2003 sample consisted of 71 individuals, 64 of which were adults. In 2004, we again completed 71 captures, including the recapture of 50 individuals from the previous year. Thus, we completed a total of 142 captures across the two year period, and the data we present are based on 92 individuals, 83 of which are adults (including subadults captured in 2003 that were recaptured as adults in 2004). We define subadults as individuals in their second year of life, determined by dental eruption (following Eaglen, 1985) and immature sexual characteristics (Sauter et al., 2002). The oldest individual in the study sample is Orange 156 at 16 years of age in 2004 (Sauter et al., in preparation), which approaches the maximum known life span at Beza Mahafaly (Gould et al., 2003). Within our sample, only two other individuals of known age exceed 10 years of age [Yellow 489 and Black 432 (Sauter et al., in preparation)]. Preliminary demographic data for our study population indicate that young or prime adults represent 70% of our sample, with the remainder consisting of either old or subadult individuals [Sauter and Cuozzo (unpublished data); see Sauter et al. (2002) for criteria used to determine age grades]. These demographic data correspond to earlier studies of this population, in which the majority of individuals consisted of young and prime adults (e.g., Sussman, 1991).

Individual lemurs were captured using a Telinect blow dart system (Telinect USA, Inc., Agua Dulce, California, USA) and a drug mixture of 20–60 mg of ketamine hydrochloride

(Ketaset, Fort Dodge Laboratories, Fort Dodge, Iowa, USA) and 0.1–2.0 mg of diazepam (Valium, Roche Inc., F-92521 Neuilly-s/Seine, CEDEX, France). Doses were determined based on protocols developed over 17 years and over 360 captures of ring-tailed lemurs at Beza Mahafaly (e.g., Sauter et al., 2001, 2002, 2006; Miller et al., in press).

All captures occurred as early as possible in the morning to allow each lemur adequate time to recover before being released prior to nightfall on the same day. A trained veterinarian and/or veterinary students were on-site to monitor the health of each individual lemur. After data were collected, lemurs were placed in covered dog kennels, and kept in a quiet place for recovery. Upon recovery, individuals were released in the area where originally captured (normally within six hours). Following standards outlined by the U.S. CITES Management Authority (a unit of the U.S. Fish and Wildlife Service), each member of the research team wore protective surgical masks and gloves during data collection in order to preclude disease transfer while handling lemurs. All methods and materials received approval by and followed standard animal handling guidelines of the Institutional Animal Care and Use Committee (IACUC) of the University of Colorado.

Upon immobilization, the dentition of each individual was examined and the degree of tooth loss was scored. Teeth were recorded as missing if either no trace of the tooth was present (i.e., no evidence of roots), or if the tooth crown was absent, with only roots remaining (worn down to or below the gumline) (Fig. 1a). This latter category differs from the scoring of missing teeth in skeletal or fossil specimens (e.g., Schultz, 1935; Lovell, 1990), as remodeling of the alveoli is not visible in living animals. This distinction is important for our later comparisons, as most published data on primate tooth loss come from skeletal samples (e.g., Schultz, 1935; Lovell, 1990). Tooth positions represented by partial and/or worn roots are best thought of as being “functionally absent” teeth because no portion of the tooth remains in functional occlusion. In addition, one or more of the roots of the remaining portions of these “functionally absent” teeth often show alveolar damage in ring-tailed lemur skeletal specimens (Cuzzo and Sauter, 2004, in preparation). Teeth retaining any part of the crown, regardless of how damaged or worn, were not scored as absent. To preserve a permanent record for each individual, and as part of our long-term research program on dental health, tooth wear, ecology, behavior, and life history, we collected complete sets of dental impressions for each lemur. Impressions were made of both the left and right maxillary and mandibular tooth rows, as well as the toothcomb. Dental impressions were made using custom-built impression trays and President Jet Regular Body polyvinylsiloxane impression material (Coltene-Whaledent, Mawah, New Jersey, USA).

In addition to the 83 living individuals studied, we examined the 25 craniodental specimens in the Beza Mahafaly Osteological Collection (BMOC) housed in the small museum at the Beza Mahafaly reserve. *Lemur catta* craniodental specimens in the BMOC sample consist of: 1) complete or partial crania with one or both associated jaws ($n = 11$), 2) complete

or partial crania without associated jaws ($n = 12$), and 3) isolated jaws without an associated cranium ($n = 2$). Among these 25 individuals, two are clearly not adult [BMOC 68 is a ca. 4-month-old infant, with adult maxillary and mandibular first molars formed in their crypts and M^1 just beginning to erupt (ring-tailed lemur adult M^1 erupts in month four; Eaglen, 1985); BMOC 63 is the cranium of a 9–10-month-old juvenile with the alveoli for left and right M^1 intact (both M^1 were lost postmortem), alveoli for left and right M^2 incompletely ossified but both teeth erupted, and adult P^4 having not yet erupted (which occurs at 12 months in *Lemur catta*; Eaglen, 1985)]. Among the remaining 23 adult specimens, all ages are represented, with at least one third of the individuals exhibiting only light-to-moderate tooth wear, consistent with the patterns seen among living young adults of known age at Beza Mahafaly (Cuzzo and Sauter, in preparation). Therefore, this sample closely corresponds to the “death assemblage” of the living population, with a large number of younger individuals. This would be expected given the concave mortality curves seen among primates [e.g., in sympatric *Propithecus verreauxi*, a high proportion of younger individuals do not survive long into adulthood (Richard et al., 2002)]. We examined each specimen in detail, including those recovered by our research team, over two field seasons (2003–2004) at Beza Mahafaly for evidence of dental pathology, and recorded patterns of severe wear and antemortem tooth loss. We also examined 73 *Propithecus verreauxi* cranial and/or mandibular specimens in the BMOC for evidence of tooth loss. Data for the sifaka sample were scored following the criteria outlined above for *Lemur catta*.

Results

Table 2 presents the frequency of individual ring-tailed lemurs missing teeth by their percentage of tooth loss. The two individuals with the most excessive tooth loss exhibit 69% (Blue 132) and 81% (Orange 170) loss, respectively. Data on extant primate tooth loss have been published in two ways: 1) by number of individuals in a sample missing teeth

Table 2

Percentage of antemortem tooth loss in individual ring-tailed lemurs at Beza Mahafaly Special Reserve ($n = 83$)

Antemortem tooth loss % ^a	Number and percentage of individuals in each category
0	61 (73.5%)
1–10	9 (10.8%)
11–20	4 (4.8%)
21–30	1 (1.2%)
31–40	3 (3.6%)
41–50	1 (1.2%)
51–60	2 (2.4%)
61–70	1 (1.2%)
71–80	0
81–90	1 (1.2%)
91–100	0

^a % tooth loss represents the number of teeth missing in an individual divided by the total of number of tooth positions (36) and multiplied by 100.

and 2) by the total number of missing teeth in a given sample. Table 3a compares the percentage of individuals exhibiting at least one missing tooth in this population of ring-tailed lemurs with data adapted from published descriptions of other extant primates. Only the 29.2% for *Gorilla gorilla* exceeds the 26.5% for ring-tailed lemurs at Beza Mahafaly ($n = 83$). In contrast, only 5.5% of sympatric *Propithecus verreauxi* at Beza Mahafaly exhibit a missing tooth. Table 3b shows the total number of teeth scored as missing in this population compared to data for other extant primates. In our current sample, 192 teeth were scored as missing. This represents 6.4% of the 2988 total tooth positions examined (83 individuals, 36 tooth positions per individual). Of the additional primates included, only *Cebuella pygmaea* (Herskovitz, 1970) exceeds 1% absence of observed teeth. Among sympatric *Propithecus verreauxi*, five of 937 tooth positions (0.5%) were scored as absent.

Figure 2 presents the frequency of tooth loss by tooth position in *Lemur catta*. The most frequently missing tooth position is M1 followed by P4, P3, and then M2. The most frequently missing tooth positions are adjacent to each other, and are centered in a single area of the mouth (see discussion). As seen in Figures 3 and 4, which present the distribution of tooth loss frequency based on eruption order for the maxillary and mandibular dentitions, respectively (Eaglen, 1985), several tooth positions (M^3 and P_2) had no teeth scored as missing in our sample. These figures also illustrate that, although the most frequently missing teeth are the first to erupt (M_1 and M^1), there is not a clear correspondence between eruption order and frequency of tooth loss for the remaining tooth positions (e.g., M_3 erupts late, yet is often lost).

Table 4 presents a comparison of the degree of tooth loss between 2003 and 2004 for individuals recaptured who exhibited tooth loss in 2004 ($n = 16$). Orange 170, an adult male who displayed 61% tooth loss in 2003 (Cuzzo and Sauter, 2004), experienced an increase in tooth loss to 81% in slightly less than 12 months. The rapid increase in tooth loss in this individual included the loss of two of the three teeth remaining in the toothcomb in 2003. As a result, this individual has only one tooth (the left canine) remaining in the

Table 3b

Number and percentage of missing teeth in *Lemur catta* compared to other samples of extant primates

Taxon	Number of teeth in sample ^a	Number of missing teeth in sample	Percentage of missing teeth in sample
<i>Lemur catta</i>	2988	192	6.43%
<i>Cebuella pygmaeus</i> ^b	2304	27	1.17%
<i>Alouatta palliata</i> ^c	4932	32	0.65%
<i>Callithrix</i> (3 species) ^b	4800	30	0.63%
<i>Propithecus verreauxi</i> ^d	937	5	0.53%
<i>Pongo pygmaeus</i> ^e	2794 ^f	12	0.43%
<i>Ateles geoffroyi</i> ^c	2304	9	0.39%
<i>Saguinus</i> (10 species) ^b	21,824	64	0.29%
<i>Cebus capucinus</i> ^c	3024	8	0.27%

^a Number of teeth = number of specimens multiplied by the number of tooth positions per taxon (e.g., *Lemur catta*: $n = 83 \times 36$ tooth positions).

^b Data adapted from Herskovitz (1970).

^c Data adapted from Smith et al. (1977).

^d Data for *Propithecus verreauxi* from BMOC sample collected by the authors. Number of teeth = number of teeth scored by the authors (premolars and molars only). Tooth absence scored following methods described for *Lemur catta* in text.

^e Data adapted from Stoner (1995).

^f Number of teeth = number of teeth scored in Stoner (1995).

toothcomb. Other individuals experiencing a noticeable increase in tooth loss between 2003 and 2004 include Black 432 (from 25% to 36%), Pink I 143 (from 6% to 19%), and Blue 132 (from 56% [Cuzzo and Sauter, 2004] to 69%).

Table 5a presents data on tooth loss in the ring-tailed lemur skeletal sample from the Beza Mahafaly Osteological Collection. Of the 23 adult specimens in this collection, four (17.4%) exhibit unequivocal alveolar damage and bone remodeling. Of these 23 specimens, BMOC 98 displays the highest frequency of tooth loss (Fig. 5). This individual lost at least seven of 18 (39%) maxillary teeth antemortem (right I^1 , P^3 , P^4 , M^1 , M^2 , and left M^1 , M^2) based on observed alveolar damage and/or bone remodeling. In addition, three other teeth (left and right M^3 and left P^4) show some alveolar damage and/or remodeling, with these teeth likely being at least “functionally absent” (as defined earlier). Therefore, it is probable that this individual had lost 10 of 18 maxillary teeth (56%) antemortem,

Table 3a

Percentage of ring-tailed lemurs missing at least one tooth compared with other samples of extant primates

Taxon	Number of specimens	Number of specimens with tooth loss	Percentage of specimens with tooth loss
<i>Gorilla gorilla</i> ^a	65	19	29.2%
<i>Lemur catta</i>	83	22	26.5%
<i>Pan troglodytes</i> ^a	30	5	16.7%
<i>Ateles geoffroyi</i> ^b	64	7	10.9%
<i>Cebus capucinus</i> ^b	84	7	8.3%
<i>Pongo pygmaeus</i> ^a	34	2	5.9%
<i>Propithecus verreauxi</i> ^c	73	4	5.5%

^a Hominoid data from Cuzzo and Sauter (2004; adapted from Lovell, 1990).

^b Platyrrhine data adapted from Smith et al. (1977).

^c Data for *Propithecus verreauxi* collected from BMOC sample by the authors.

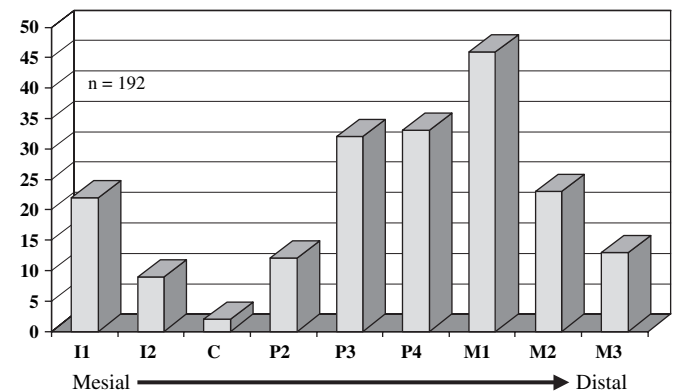


Fig. 2. Frequency of missing teeth in living ring-tailed lemurs distributed by tooth position.

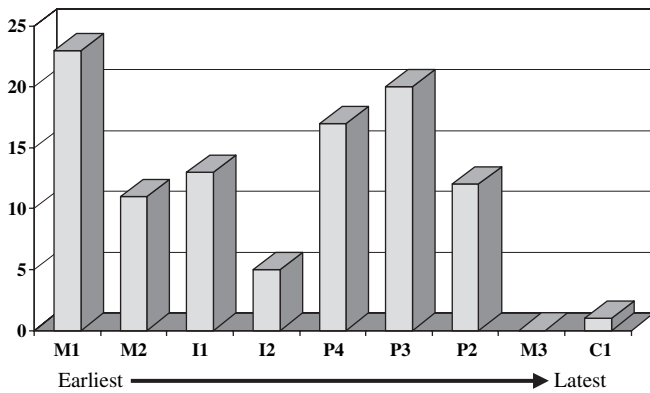


Fig. 3. Maxillary tooth loss frequencies ranked by eruption order.

a value comparable to several of the more impaired individuals in our living sample. Table 5b presents information on tooth loss in the BMO *P. verreauxi* sample. Of the 73 sifaka specimens examined, two (2.7%) display alveolar damage and subsequent tooth loss (BMO 18 and 28), with both individuals missing an M³ (Fig. 6). In addition, two other individuals exhibit “functionally absent” teeth (BMO 121 and 137).

Discussion

Causes of tooth loss

Feeding ecology. Ring-tailed lemurs display a high frequency of tooth loss when compared to other nonhuman primates (Table 3). In our study, only gorillas have a percentage of individuals with tooth loss (29.2%) that exceeds the 26.5% in ring-tailed lemurs (Table 3a). When comparing tooth loss based on the number of teeth missing in samples of nonhuman primates (Table 3b), ring-tailed lemurs have by far the highest percentage of missing teeth (6.4%). The diet of ring-tailed lemurs living in riverine gallery forests is dominated by tamarind fruit (e.g., Jolly, 1966; Sauter, 1992, 1998; Sauter et al., 2002; Simmen et al., 2006), which has a hard, tough outer casing (Yamashita, 2000, in preparation). In fact, ripe tamarind pods are the hardest and toughest of all foods eaten by ring-tailed lemurs at Beza Mahafaly (Yamashita, 2000, in

Table 4

Changes in the percentage of tooth loss between 2003 and 2004 among individual living ring-tailed lemurs displaying tooth loss in 2004

Individual ^a	Date captured 2003	% tooth loss ^b 2003	Date captured 2004	% tooth loss ^b 2004	% change in tooth loss 2003–2004
Black 111	June 10	0%	July 11	3%	3%
Yellow 489	July 4	0%	July 12	3%	3%
Blue 136	July 2	3%	July 15	3%	0%
Teal 151	July 20	3%	July 2	3%	0%
Blue 141	July 23	3%	July 4	6%	3%
Orange 156	June 13	3%	July 7	6%	3%
Black 117	July 8	6%	July 7	14%	8%
Blue 127	July 23	6%	July 17	14%	8%
Orange 166	July 1	8%	July 9	17%	9%
Pink I 143	July 9	6%	July 3	19%	13%
Black 432	June 12	25%	June 30	36%	11%
Blue 138	July 4	28%	June 16	36%	8%
Blue 139	July 10	31%	July 4	39%	8%
Yellow 195	July 3	50%	July 5	56%	6%
Blue 132	June 29	56%	June 16	69%	13%
Orange 170	July 6	61%	June 27	81%	20%

^a Individual lemurs ordered by % tooth loss in 2004.

^b % tooth loss represents the number of teeth missing in an individual divided by the total of number of tooth positions (36) multiplied 100.

preparation). As tamarind reproduces asynchronously, it is available year round, including during the marked dry season when few other foods are readily or continually available, and thus they are an important fallback food (Sauter, 1998). Ring-tailed lemurs pass hard tamarind seeds through the digestive system mostly intact (e.g., Yamashita, 2000; Simmen et al., 2006). Accessing these seeds, primarily to remove the surrounding pulp (i.e., the mesocarp) is an intensive process, and leaves an obvious record on their teeth. Processing of large tamarind pods initially occurs in the region of the first molars and adjacent premolars (Fig. 7). In order to access the enclosed seeds, the lemur repeatedly bites down on the pod in order to initiate crack formation (Cuzzo and Sauter, 2006). In addition, removal of the pulp-covered seeds from the pod requires additional tooth use, with the hard, tough outer casing, and the tough internal fibers of the fruit repeatedly contacting the surface of the teeth. Although they are usually passed through the digestive system intact, seeds recovered from fecal samples at Beza Mahafaly often exhibit evidence (i.e., tooth marks) of this process (Cuzzo and Sauter, personal observation). In addition, the internal fibers (Fig. 8) are continually scraped across the enamel surface, and sometimes are pulled between the teeth (Cuzzo and Sauter, personal observation), leaving distinct interstitial wear facets, at times accompanied by receding gingiva and bone loss (Fig. 9). The combination of processing the hard, tough outer casing of large tamarind fruit and the continual scraping of tough internal fibers across thin enamel likely contributes to the high frequency of excessive wear and subsequent tooth loss in this region of the mouth (Fig. 2).

In contrast to *Lemur catta* at Beza Mahafaly, sympatric *P. verreauxi* (which also has thin enamel; Table 1) exhibits far less wear and tooth loss (Tables 3a, b, 5b). Among the 73 BMO specimens examined, only four individuals (5.5%)

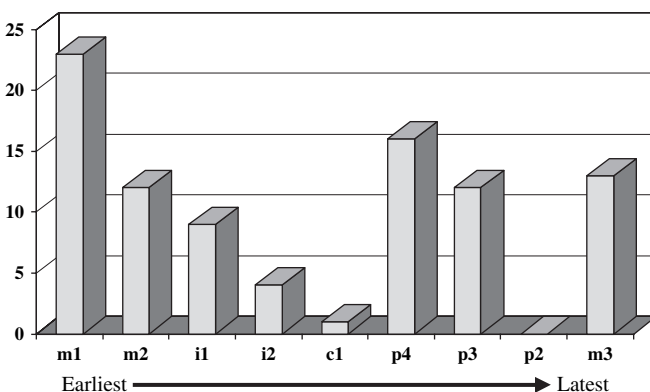


Fig. 4. Mandibular tooth loss frequencies ranked by eruption order.

Table 5a

Tooth-loss data for individual ring-tailed lemurs in the Beza Mahafaly Osteological Collection

Tooth loss	<i>n</i>	<i>n</i> with tooth loss	% with tooth loss
Antemortem tooth loss (alveolar damage and/or remodeling only)	23	4	17.4%
Antemortem tooth loss (alveolar evidence and “functional” loss) ^a	23	8	34.8%

^a See text for discussion of “functional” tooth loss.

exhibited tooth loss. Although dentally adapted to folivory, Verreaux’s sifaka regularly consume tamarind fruit (e.g., Yamashita, 2002). However, unlike ring-tailed lemurs, *Propithecus verreauxi* primarily utilizes softer and less tough unripe tamarind pods (Yamashita, 2000). Both sifaka specimens displaying alveolar damage and bone remodeling (BMOC 18 and 28) had lost an M³. The M³ [which is reduced in sifakas (e.g., Tattersall, 1982; Swindler, 2002)] was lost in these specimens due to dental damage and/or disease, as the remaining teeth in each specimen did not exhibit severe tooth wear (Fig. 6). Among ring-tailed lemurs, tooth loss often occurs in high numbers in individuals, with frequent tooth loss usually accompanied by severe wear in adjacent teeth (Fig. 1a). Thus, *Propithecus verreauxi* at Beza Mahafaly displays a pattern of tooth loss more similar to other primates, in which tooth loss most often results from dental damage and/or disease rather than food processing and wear (e.g., Schultz, 1935; Smith et al., 1977; Lovell, 1990).

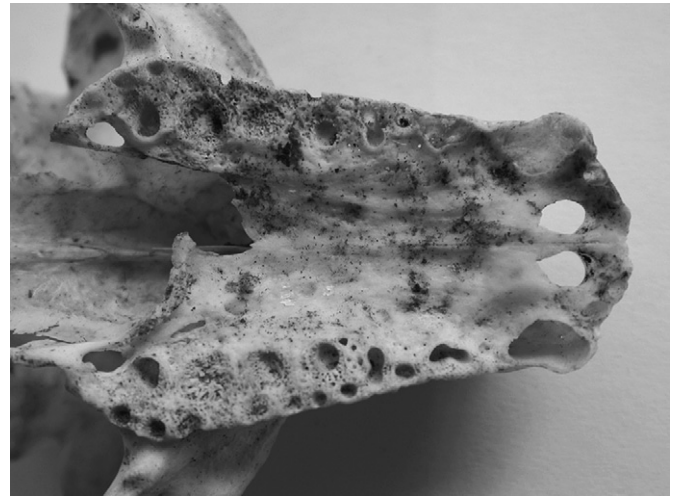
A similar contrast in the pattern of tooth loss between sympatric ring-tailed lemurs and Verreaux’s sifaka is seen when ring-tailed lemurs are compared to other extant primates (Smith et al., 1977; Lovell, 1990). Figure 10 compares the number and distribution of missing teeth among ring-tailed lemurs with those from a sample of howler monkeys (Smith et al., 1977). In the howler monkey (*Alouatta palliata*) sample, most of the 32 missing teeth are found in the anterior dentition (incisors and canines), and many were likely lost due to periodontal disease resulting from damage incurred during male aggression (Smith et al., 1977). As described above, the majority of the 192 missing teeth among ring-tailed lemurs are found in the distal portion of the mouth where food is primarily processed.

The sequence of dental eruption in ring-tailed lemurs plays a limited role in their pattern of tooth wear and loss. As seen in Figures 3 and 4, which present the frequency of tooth loss ranked by eruption order, first molars are the most frequently

Table 5b

Tooth-loss data for individual Verreaux’s sifaka in the Beza Mahafaly Osteological Collection

Tooth loss	<i>n</i>	<i>n</i> with tooth loss	% with tooth loss
Antemortem tooth loss (alveolar damage and/or remodeling only)	73	2	2.7%
Antemortem tooth loss (alveolar evidence and “functional” loss) ^a	73	4	5.5%

^a See text for discussion of “functional” tooth loss.Fig. 5. Antemortem tooth loss ($\geq 56\%$) as determined by alveolar remodeling in BMOC 98.

missing teeth in both the maxillary and mandibular dentition. As first molars erupt at four months of age in ring-tailed lemurs (Eaglen, 1985), corresponding to the age at weaning and the transition to an adult diet (e.g., Godfrey et al., 2001), the high frequency of wear and subsequent loss is not a surprise. The low frequency (or even absence) of loss of P₂, M³, and C¹ corresponds to their late eruption (Eaglen, 1985). However, most teeth lost are those used in processing tamarind, and do not correspond to their sequence of eruption. Although second molars, maxillary incisors, and the tooth-comb (which includes I₁, I₂, and C₁) all erupt prior to the premolars, P³ and P⁴ are exceeded in their frequency of absence only by M¹. Among the mandibular teeth, P₄ is more frequently lost than M₂, M₃, or the teeth constituting the tooth-comb. As noted above, tamarind fruit is primarily processed in the region of the first molars and premolars (Fig. 7). Despite their later eruption, P₃ and P₄ are more often absent than those teeth that erupt earlier (Figs. 2–4). It is also telling that two of the teeth displaying infrequent loss (caniniform P₂ and C¹) are

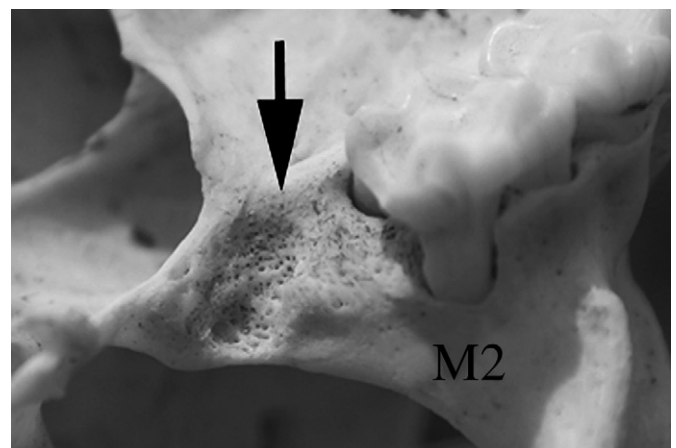
Fig. 6. Missing M³ in *Propithecus verreauxi* (black arrow illustrates remodeling of the alveolus) (BMOC 28). Note the limited wear in adjacent M².



Fig. 7. A ring-tailed lemur processing a tamarind pod (white arrow).

not generally associated with food processing, except in individuals with severe dental impairment (Cuozzo and Sauter, 2006). Although M^3 is sometimes used to process food, its relatively small size, combined with its position in the mouth, precludes significant contact during the initial processing of large tamarind fruit (Cuozzo and Sauter, 2006, personal observation). When combined with late eruption, its limited role in processing hard, tough foods (in contrast to the elongated crown of M^3) likely leads to its rare loss in this population, with the only definitive example of a missing M^3 being that seen in BMOC 64 (Fig. 11). In contrast, the only two sifaka teeth scored as missing based on alveolar damage and remodeling are maxillary third molars (BMOC 18 and 28;

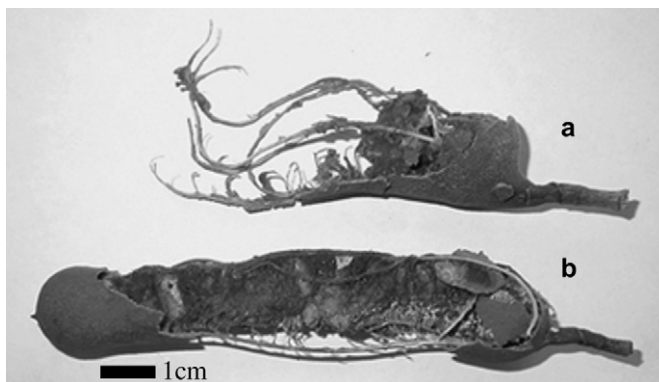


Fig. 8. Fruit of the tamarind tree (*Tamarindus indica*): note the internal fibers. (a) Tamarind that has been processed by a ring-tailed lemur and discarded. (b) Tamarind fruit with outer casing intentionally removed to show the internal structure.

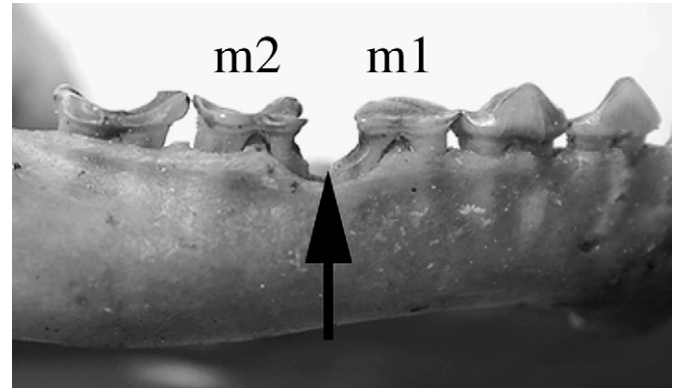


Fig. 9. Severe interstitial wear in BMOC 67.

Fig. 6). Finally, despite their small size and derived morphology, maxillary and mandibular incisors are frequently lost, although not as often as those later erupting teeth used in processing tamarind fruit (i.e., P^3 , P^4 , and M^1). The frequent loss of incisors can be attributed to wear resulting from 1) their role in stripping certain types of vegetation (e.g., Sauter et al., 2002; Yamashita, 2003) and 2) in the case of the mandibular incisors, their significant grooming function (e.g., the removal of ectoparasites) as part of the toothcomb (Sauter et al., 2002; Cuozzo et al., in preparation). Thus, the frequency of loss for most tooth positions in ring-tailed lemurs does not correspond to their order in the eruption sequence. Rather, our data strongly suggest that the frequent absence of most teeth is related to their function.

Dental erosion. In addition to the mechanical properties of foods, their chemical composition may also impact tooth loss. Dental erosion is the chemical deterioration of the dentition (e.g., Gandara and Truelove, 1999; Lussi et al., 2004; Shipley et al., 2005). Chemical erosion of teeth is a major issue confronting modern humans due to a variety of dietary and behavioral causes, including the consumption of acidic foods (e.g., Verrett, 2001; Lussi et al., 2004; Shipley et al., 2005). Chemical erosion resulting from an acidic diet has also been

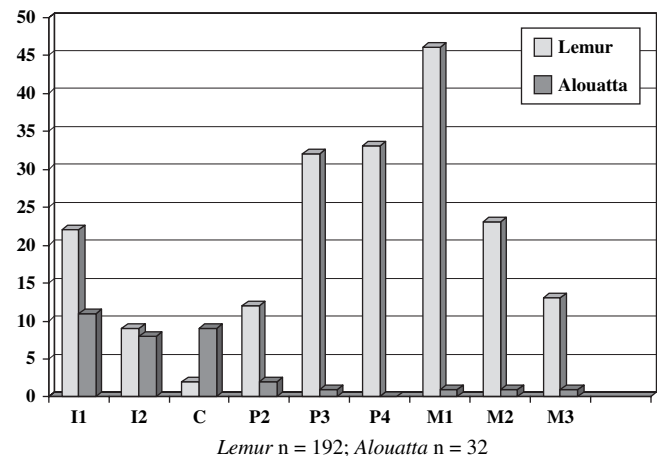


Fig. 10. Frequency of missing teeth distributed by tooth position compared between *Lemur catta* and *Alouatta palliata* (Alouatta data adapted from Smith et al., 1977).

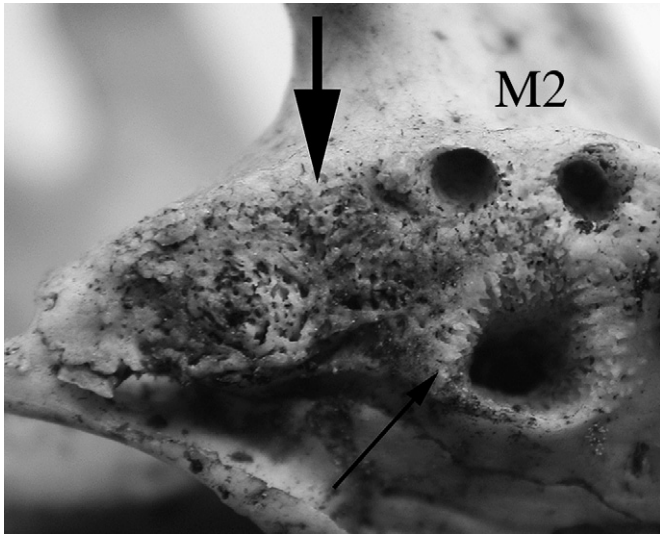


Fig. 11. Missing M^3 in BMOc 64. The large arrow illustrates the position of absent M^3 , while the small arrow points to remodeling of the lingual alveolus of M^2 .

suggested as the cause of dental wear in the extinct lemur *Pachylemur* (e.g., Vasey et al., 2005; Godfrey et al., 2006). However, acidity of food alone is not predictive of dental erosion (e.g., Lussi et al., 2004; Shipley et al., 2005), as saliva may buffer the impact of acidic foods, thereby reducing demineralization and tissue loss (Lucas, 2004; Shipley et al., 2005).

Although tamarind fruit is highly acidic (e.g., Gunasena and Hughes, 2000; Khandare et al., 2000; Pino et al., 2004), and may well be a compounding factor in the patterns of tooth wear seen in ring-tailed lemurs, the patterns of wear and subsequent tooth loss we describe are more likely related to food processing and the mechanical properties of tamarind fruit than to chemical erosion. First, the frequency of teeth lost in our sample does not directly correspond to the sequence of dental eruption. Both P_3 and P_4 are more frequently lost than is M_2 , which erupts earlier than either of these premolars. Ring-tailed lemurs begin eating tamarind fruit early in life, and we have observed young individuals (those between eight and ten months of age) processing this food (Cuozzo and Sauter, unpublished data). Tooth wear is also apparent in these young individuals, as seen in BMOc 63 in which dp^4 displays obvious wear (Fig. 12a), especially when compared to individuals that have not yet been weaned (Fig. 12b). If chemical erosion is largely responsible for these patterns of wear, one would expect that the deterioration, wear, and eventual loss of permanent teeth would correspond to the sequence of eruption, as those teeth that erupt earlier (i.e., M_2) would be subject to chemical erosion for a longer period of time and hence be more prone to destruction. In addition, the consumption of tamarind fruit is responsible for the presence of dark stains on ring-tailed lemur teeth (e.g., Sauter et al., 2002). As these dark stains indicate the areas where tamarind pulp (and thus its acidic components) adheres to tooth surfaces, one would expect that erosion would most often occur in these areas. Yet, the area in which the most substantial staining

occurs is not where teeth are most frequently worn and/or lost, but it is instead concentrated in anterior tooth positions (the maxillary canines and caniniform P_2), which are rarely missing and are not usually used in food processing [except in individuals with severely impaired dentitions (Cuozzo and Sauter, 2006)]. Also, although sympatric Verreaux's sifaka regularly consume tamarind fruit (Yamashita, 2002), they exhibit far less wear and fewer missing teeth when compared to ring-tailed lemurs at BMSR. At BMSR, *P. verreauxi* primarily use unripe tamarind fruit (Yamashita, 2000). Ripe tamarind fruit is harder and tougher than unripe tamarind fruit (Yamashita, 2000). However, the level of acidity in tamarind fruit does not change as it matures (Gunasena and Hughes, 2000). Therefore, the difference between the degree of tooth wear and loss in ring-tailed lemurs and sympatric Verreaux's sifaka at BMSR is not likely a result of tamarind acidity, but rather a product of the mechanical properties of tamarind, as ring-tailed lemurs primarily process harder and tougher ripe tamarind fruit. Finally, the fact that tamarind pods are processed in the area of greatest wear and loss (Figs. 2 and 7) strongly

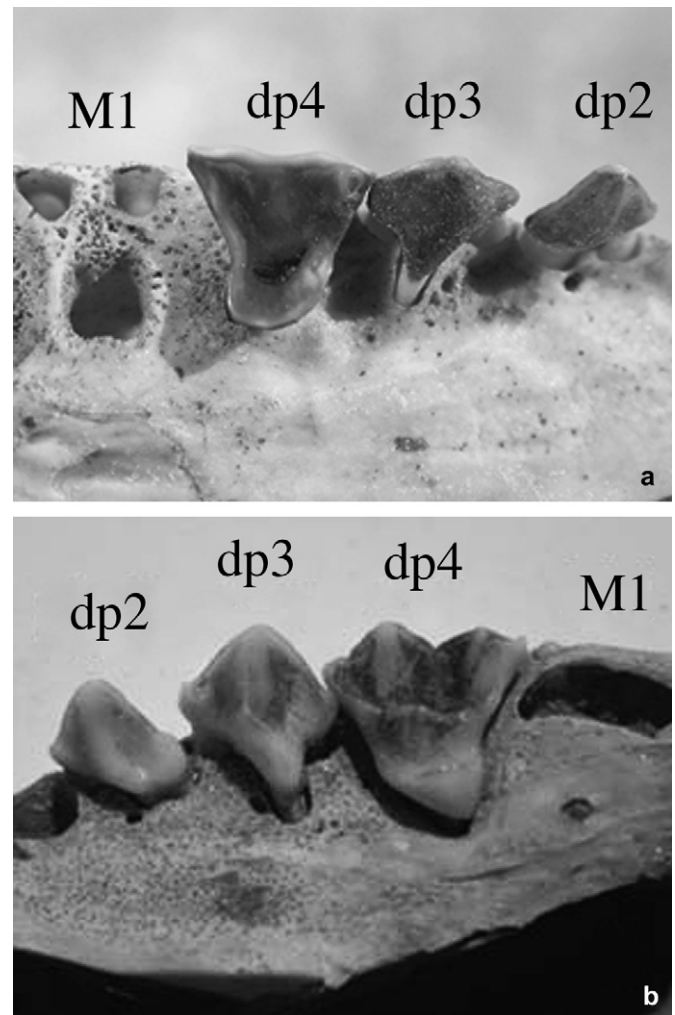


Fig. 12. (a) Worn dp^4 in BMOc 63, a ca. 9–10-month-old ring-tailed lemur. (b) Unworn dp^4 in a newly recovered, preweaned (ca. 3–4-month-old) ring-tailed lemur (BMOc 136).

suggests that food processing, rather than chemical erosion, is largely responsible for the patterns of tooth wear and loss seen in this ring-tailed lemur population.

Dental structure. As noted earlier, tooth wear is the result of a complex interaction of variables (e.g., Maas and Dumont, 1999). One important variable in the pattern of ring-tailed lemur tooth loss is enamel quantity, as ring-tailed lemurs have among the thinnest enamel of all primates (Table 1) (e.g., Shellis, et al., 1998; Martin et al., 2003; Godfrey et al., 2005). In a study of great ape tooth wear, Dean et al. (1992) noted that wear was both delayed and less pronounced in thick-enamelled orangutans as compared to thin-enamelled chimpanzees and gorillas. In general, thick enamel corresponds to a diet dominated by hard and/or tough foods, although this relationship is far from perfect (e.g., Kay, 1981, 1985; Dumont, 1995; Shellis et al., 1998; Maas and Dumont, 1999; Teaford and Ungar, 2000; Martin et al., 2003; Godfrey et al., 2005; Liu and Zheng, 2005). In addition to enamel quantity, the internal structure of enamel, for example the presence of decussating (i.e., differentially oriented) enamel prisms (e.g., Janis and Fortelius, 1988; Maas, 1994; Maas and Dumont, 1999; Martin et al., 2003; Godfrey et al., 2005) is thought to provide resistance to crack propagation (e.g., Maas and Dumont, 1999; Martin et al., 2003; Godfrey et al., 2005). Although enamel decussation occurs in primates with both thin and thick enamel (e.g., Maas and Dumont, 1999), it is often associated with thick-enamelled, hard-object feeding primates such as the subfossil Malagasy strepsirrhine *Archaeolemur* (Godfrey et al., 2005). As noted by Martin et al. (2003), the presence of thick enamel is not a prerequisite for a hard-food diet, as initial placement of food and enamel structure (e.g., amount of decussation) each play a role in feeding. For example, *Chiropotes* and *Pithecia*, despite having thin enamel, possess well defined enamel decussation (Martin et al., 2003) and utilize a hard-food diet. In addition to enamel decussation, these primates initially open hard foods with their canines, and process the soft inner portions with their thin-enamelled postcanine teeth.

Given their thin enamel and a diet dominated by a hard, tough fallback food, it is not unexpected that ring-tailed lemurs living in riverine gallery forests experience significant tooth wear. However, as approximately 90% of ring-tailed lemur enamel consists of decussating prisms (Maas, 1994), which are thought to resist crack propagation and enamel damage, the excessive wear seems aberrant. Despite displaying thin enamel and significant decussation reminiscent of the pitheciin pattern described by Martin et al. (2003), ring-tailed lemurs primarily process hard, tough foods with their postcanine teeth, which are frequently lost due to excessive wear. The pattern of severe wear and tooth loss in ring-tailed lemurs also contrasts with the recent argument by Lambert et al. (2004), in which hard fallback foods are described as an important selective variable in the evolution of thicker enamel in the grey-cheeked mangabey (*Lophocebus albigena*).

As thicker enamel increases the functional longevity of teeth (e.g., Janis and Fortelius, 1988; Lucas, 2004), the apparent paradox between tooth wear and enamel thickness at Beza

Mahafaly suggests the possibility that ring-tailed lemurs living in tamarind dominated gallery forests may have only recently become dependent on tamarind fruit as a key fallback food source. This scenario is likely given the rapid pace at which primate dental enamel thickness may evolve (Hlusko, 2004). Among primates, thin enamel is often adaptive. For example, data from a number of folivorous primates, as well as marsupial koalas among other mammals (e.g., Lanyon and Sanson, 1986; Logan and Sanson, 2002), illustrate that thin enamel responds to wear with increased cutting edges, thereby maintaining dental function for a continued period of time (e.g., Kay, 1981; Ungar and Williamson, 2000; King et al., 2005). The presence of thin enamel in ring-tailed lemurs may therefore represent past selection for enamel thinness. In an earlier study of lemur dental morphology, Yamashita (1998) noted that *L. catta* has long molar crests and acute cusps when compared to other lemurids (i.e., *Eulemur rubriventer*), traits often associated with folivory (e.g., Seligsohn, 1977). In addition, the large cecum of ring-tailed lemurs is consistent with folivory, as it is required for the microbial breakdown of plant material (Campbell et al., 2000). Extant ring-tailed lemurs are best described as opportunistic omnivores (Sauter et al., 1999). However, although not exhibiting the degree of morphological specialization seen in folivorous *Propithecus*, comparative data, particularly enamel thickness and molar morphology, suggest the possibility that ring-tailed lemurs may have previously relied on folivory as a fallback diet.

Why would ring-tailed lemurs now exploit resources for which they are not mechanically adapted? For almost two millennia, human activity has dramatically impacted the environment of Madagascar (e.g., Godfrey et al., 1997; Godfrey and Jungers, 2003a; Burney et al., 2004). Due to habitat destruction, and even human predation, Madagascar's faunal diversity has been radically reduced (Godfrey and Jungers, 2002, 2003b; Burney et al., 2004; Perez et al., 2005), with all of the once plentiful megafauna (including "giant" lemurs) becoming extinct over the past thousand years. Although many smaller species of lemur (less than 10 kg) have survived this human-induced change, it is likely that extant species now exploit altered, if not completely different niches than those in which they evolved. *Lemur catta* may be one such species.

As noted earlier, recent work on the genetics of primate dental enamel thickness suggests that it can quickly respond to selective pressures and dietary shifts (Hlusko, 2004), yet ring-tailed lemurs retain thin-enamelled teeth. The long-term consequences of thin-enamelled lemurs at Beza Mahafaly consuming a mechanically challenging food such as tamarind fruit are readily apparent in their severe wear and tooth loss, which correspond to suboptimal nutritional levels and biomedical values in members of the population exhibiting such wear (Miller et al., in press; Sauter et al., 2006). Advanced stages of wear may also correspond to reduced fitness in lemurs, as suggested for *Propithecus edwardsi* (King et al., 2005). Taken together, the incongruity between thin enamel and a hard, tough diet suggests that ring-tailed lemurs living in tamarind dominated riverine gallery forests such as Beza Mahafaly may now be exploiting resources and/or habitats not used in

the past. Given the tremendous impact human activity (e.g., deforestation) has had on Madagascar's natural environment, this scenario is quite plausible.

As dental and long-term ecological data are only available for ring-tailed lemurs living in two gallery forests in which tamarind is a key fallback food [Beza Mahafaly and the Berenty Reserve in southeastern Madagascar (e.g., Jolly, 1966; Sauther et al., 1999)], it is imperative to obtain data on food availability and tooth use for ring-tailed lemurs living in areas where tamarind is neither dominant nor available. Ring-tailed lemurs have a very broad spatial distribution throughout southern Madagascar (Goodman et al., 2006), ranging from the dry southwestern coastal plain (Dutton et al., 2003) to the high-altitude (>2500 m) Andringitra Massif (Goodman and Langrand, 1996). Although not documented in detail, the pattern of severe wear and tooth loss seen at Beza Mahafaly has also been noted at Berenty (Crawford, personal communication; Soma, personal communication), the only other location where long-term ecological data are available for ring-tailed lemurs, and, importantly, where tamarind is also dominant. In order to test whether the patterns of wear in these two areas are due to food processing and the mechanical properties of tamarind, we plan to collect data on dental health and tooth wear, in addition to information on feeding ecology, food availability, and mechanical properties, in areas inhabited by ring-tailed lemurs where tamarind is rare.

Individual life history

Tooth loss over time in known individuals. As most studies of primate dental health and tooth loss come from skeletal samples (see earlier references), there is a paucity of longitudinal data available on tooth loss among individuals. In 2004, we recaptured 50 individuals [including three lemurs originally examined in the 1990s (Sauther et al., in preparation)] from which dental data were collected in 2003. As seen in Table 4, a number of individuals missing teeth in 2003 experienced a rapid and sometimes dramatic increase in their percentage of missing teeth by 2004. Of the 50 individuals recaptured in 2004, 16 displayed tooth loss (32%). Of these 16 individuals, four (25%) experienced at least a 10% increase in their degree of tooth loss between 2003 and 2004. The most dramatic change was seen in Orange 170, whose degree of tooth loss increased from 61% to 81% in slightly less than one year (see below). As discussed by Lucas (2004), there is a presumption among those who study teeth that their loss leads to the quick death of the individual. Our data indicate that ring-tailed lemurs can experience a rapid and dramatic increase in tooth loss over a span of as little as one year, yet are able to survive.

These longitudinal data allow us to document individual dental life histories, and to examine examples of tooth loss unrelated to the pattern of tooth wear and loss seen in the overall sample. Although the majority of missing teeth in this lemur population have been lost due to use and excessive wear, several individuals have lost teeth resulting from breakage and/or disease, as in other primates (e.g., Schultz, 1935; Smith et al.,

1977; Lovell, 1990). As seen in Figures 2–4, lost canines represent only two of the 192 total missing teeth. One of the two canines is the right mandibular canine of the toothcomb in Orange 170, which was lost between 2003 and 2004. Although this tooth was present in 2003, it was recorded as being loose at the time, and was one of three of the original six teeth of the toothcomb remaining. As the ring-tailed lemur toothcomb erupts and functions as a unit (Eaglen, 1985), the loss of any part of the toothcomb apparently leads to rapid weakening and likely loss of the entire functional complex, and the one tooth remaining in Orange 170's toothcomb will not likely remain in place long. Black 432, a 13-year-old female, is the only other individual to have lost a canine. When originally captured on July 11, 1995, at approximately four years of age (Sauther et al., in preparation), she had a broken right maxillary canine. This individual was recaptured on June 12, 2003. At that time, this broken tooth had decayed, which resulted in an apical abscess presenting as an open wound on the muzzle, a condition seen in several of the living individuals (Sauther et al., 2006), as well as two skeletal specimens (BMOC 78 and 101) at Beza Mahafaly. When recaptured again on June 30, 2004, this tooth was completely lost, and only healed gingiva remained in this area of the mouth (Fig. 13). The other individual known to have lost a tooth due to damage is Black 111, whose RM₃ was broken when first examined in 2003; only the posterior portion (taloid) of the crown was present at that time. As of her recapture on July 11, 2004, this tooth had been completely lost, with only healed gingiva remaining. These examples illustrate that, while most teeth in this population are lost as a result of tooth use and excessive wear, the same types of dental pathologies that affect other primates also occur in the ring-tailed lemurs at Beza Mahafaly.

Surviving tooth loss. As discussed earlier, Lucas (2004) noted that, among dental researchers, there is a presumption that the loss of a functional dentition leads to the end of an animal's life. In contrast, our new data, combined with those previously presented for this population (Sauther et al., 2002; Cuozzo and Sauther, 2004), indicate that wild ring-tailed lemurs are able to survive for at least several years with severely impaired dentitions. The ability of ring-tailed lemurs at BMSR to survive beyond their dental senescence may result from a behavioral adaptation. During 2004, we witnessed two ring-tailed lemurs with excessive (>50%) tooth loss (Yellow 195 and Orange 170) utilizing tamarind pods that had been cracked open by other individuals and then discarded. Recall that Orange 170 exhibited 81% tooth loss (including five of six teeth in the tooth-comb) in 2004. This access to second hand food resources—provided without intention—may play a key role in the survival of dentally impaired individuals. As tamarind is a key fallback food of ring-tailed lemurs living in riverine gallery forests (e.g., Jolly, 1966; Sauther, 1992, 1998; Sauther et al., 2002; Simmen et al., 2006), the ability to feed on tamarind fruit despite severe dental impairment would be especially important during the cool dry season, as few other resources are available at that time (Sauther, 1992, 1998; Simmen et al., 2006).



Fig. 13. (a) A normal right maxillary canine. (b) A missing right maxillary canine in Black 432.

Tooth loss in the BMOC ring-tailed lemur sample

The frequency of antemortem tooth loss in the ring-tailed lemurs at Beza Mahafaly exceeds that of most extant primates for which data have been published. Because our data on tooth loss come from living animals, the types of information (e.g., alveolar damage and bone remodeling) used to identify tooth loss in skeletal specimens are not available. Hence, it may be asked whether the data we present are comparable to those from previous studies of primate skeletal samples. As seen in Table 5a, four (17.4%) of the 23 adult ring-tailed lemur specimens in the Beza Mahafaly Osteological Collection exhibit unequivocal alveolar damage and bone remodeling. Although lower than the 26.5% loss seen in the living population, this value is comparable to, or exceeds, that of all species but gorillas among other extant primate samples, as seen in Table 3a. Also, when individuals displaying “functionally absent” teeth (see earlier definition) are included, a total of eight of the 23 adult ring-tailed lemurs (34.8%) in the BMOC exhibit tooth loss, a value similar to that of the living population. In contrast, of the 73 Verreaux’s sifaka specimens in the BMOC sample (Table 5b), only two (2.7%) display alveolar damage and

subsequent tooth loss, with two additional individuals exhibiting “functionally absent” teeth. Thus, the frequency of individuals with tooth loss among sympatric Verreaux’s sifaka (5.5%) is much lower than that of either the living or BMOC ring-tailed lemur samples and likely reflects differences in feeding ecology between the two species (Cuzzo and Sauter, in preparation).

As noted earlier, BMOC 98 displays the highest frequency of tooth loss in the ring-tailed lemur skeletal sample, with this individual having lost at least seven of 18 (39%) maxillary teeth antemortem (Fig. 5). When three “functionally absent” teeth are added to the total, it is likely that this individual had lost 56% of the maxillary dentition antemortem, a value comparable to the most dentally impaired living individuals (Tables 2 and 4). As no mandible is available for this specimen, the amount of total tooth loss is unknown. However, based on the patterns seen in our living animals, it is likely that this individual experienced comparable mandibular tooth loss, especially as no living individuals and only one other BMOC specimen (BMOC 64) have lost an M³. This indicates that BMOC 98 had lost an excessive amount of teeth, even by the standards for this population. The pattern of missing teeth in this specimen closely corresponds to the pattern seen in the living sample, in that they represent the primary teeth used in processing tamarind fruit.

Implications for hominid paleobiology

The phenomenon of antemortem tooth loss and its role in interpreting hominid paleobiology has received much attention in recent years (e.g., Lebel et al., 2001; Lebel and Trinkaus, 2002; DeGusta, 2002, 2003; Holden, 2003; Cuzzo and Sauter, 2004; Lordkipanidze et al., 2005). A series of recently recovered hominid fossils, including middle Pleistocene Neandertals from Bau de l’Aubiesier, France (e.g., Lebel et al., 2001; Lebel and Trinkaus, 2002), and early Pleistocene *Homo erectus* from Dmanisi in the Republic of Georgia (Lordkipanidze et al., 2005), exhibit extreme antemortem tooth loss. The presence of this severe dental impairment has been interpreted as evidence of conspecific care, intentional care-giving, and/or human compassion (e.g., Lebel et al., 2001; Lebel and Trinkaus, 2002; Lordkipanidze et al., 2005). This window into the behavior of extinct human relatives and ancestors has also captured the public’s attention (e.g., Fischman, 2005). However, these interpretations are not beyond debate (e.g., Tappen, 1985; Dettwyler, 1991). More recently, DeGusta (2002, 2003) presented a series of arguments, based on comparative primate skeletal and dental pathology, that the dental and other physical impairments seen in fossil hominids do not exceed those in nonhuman primates. Previously, we commented on this debate (Cuzzo and Sauter, 2004), and showed that the frequency and degree of antemortem tooth loss in the Beza Mahafaly ring-tailed lemurs equals that seen in archaic hominids (e.g., Lebel and Trinkaus, 2002). Yet, new discussions of hominid paleobiology have omitted reference to recent studies of tooth loss in nonhuman primates. For example, Lordkipanidze et al. (2005), in discussing the extensive tooth loss in Dmanisi *H. erectus* specimens D3444/D3900, a cranium and associated

mandible, asserted that extreme tooth loss in nonhuman primates is rare.

Our new data on tooth loss in the Beza Mahafaly ring-tailed lemurs allow us to expand on our previous discussion (Cuzzo and Sauter, 2004) of tooth loss and hominid care-giving. The degree of tooth loss seen in l'Aubesier 11 ($\geq 81\%$) and Dmanisi D3444/D3900 (97%) has been argued to exceed that in known nonhuman primates (e.g., Lebel and Trinkaus, 2002; Lordkipanidze et al., 2005). In our sample, Orange 170, previously described as exhibiting 61% tooth loss in 2003 (Cuzzo and Sauter, 2004), displayed 81% tooth loss in 2004. As discussed earlier, this increase in tooth loss occurred over a period of less than 12 months (Table 4), and includes the additional loss of seven teeth, including two in the toothcomb. It is important to note that all of these missing teeth play a critical role in feeding, including the toothcomb (Sauter et al., 2002). This rapid loss in part reflects the complete absence of five tooth crowns, partially in place in 2003, that have since been lost, primarily through continued wear. The remaining two teeth (RC₁ and RI₂) were both present in 2003, but have since been completely lost. The degree of tooth loss in Orange 170 equals that of Tan 57, an individual with $>80\%$ tooth loss that previously survived at least three years at Beza Mahafaly (Sauter et al., 2002; Cuzzo and Sauter, 2004). Therefore, at least two individuals at Beza Mahafaly have survived with tooth loss exceeding 80%, which is comparable to that seen in both l'Aubesier 11 and Dmanisi D3444/D3900 (Lebel and Trinkaus, 2002; Lordkipanidze et al., 2005).

In addition to new data on tooth-loss frequencies, behavioral data collected during the 2004 field season, as previously discussed, provide further evidence that survival of dentally impaired primates is neither rare, nor dependent upon intentional care. It is important to note that, similar to some Pleistocene hominid populations (Lordkipanidze et al., 2005), the ring-tailed lemurs at Beza Mahafaly live in a highly seasonal, somewhat temperate environment, with extreme differences between the wet and dry seasons in both rainfall and temperature (e.g., Sauter, 1998; Ratsirarson, 2003). During the dry austral winter, overnight temperatures at Beza Mahafaly can approach 0 °C, despite being located just south of 23° south latitude. Most food resources are also dramatically reduced at this time, with only fruit and leaves of the tamarind tree available year round. Thus, tamarind is a key fallback food used during the dry season (Sauter, 1992, 1998; Simmen et al., 2006). As discussed above, we have witnessed the unintentional aid of conspecifics among the BMSR ring-tailed lemur population, where dentally impaired individuals consume tamarind fruit that has been partially processed by other group members. During the dry season, when few foods are regularly available, the ability to access this key food, despite dental impairment, would be important for long term survival (Cuzzo and Sauter, 2006).

In contrast to arguments that dentally impaired extinct hominids relied on conspecific care to survive (e.g., Lebel and Trinkaus, 2002; Lordkipanidze et al., 2005), our data show that ring-tailed lemurs with excessive tooth loss survive in part from living in a large social group, which allows

unintentional food-processing assistance. Being part of a social group also aids dentally impaired individuals to locate accessible foods, as these individuals, while sometimes existing as marginal members of their troops, often travel and feed together. This unintentional assistance is especially important, as ring-tailed lemurs do not use tools, which were available to the Dmanisi (and other) hominids for accessing and processing foods, including soft tissue such as marrow or brain (Lordkipanidze et al., 2005). Although human ancestors may well have practiced care-giving, our data show that there is no need to posit that survival of dentally impaired individuals depended on intentional care.

Conclusions

Our data on tooth wear and antemortem tooth loss in a wild population of ring-tailed lemurs attest to the importance of comprehensive, longitudinal data from single primate populations. Because these data have been collected from a location with corresponding ecological and behavioral data, we have been able to provide detailed explanations for the phenomenon of extensive wear and tooth loss that are not available from most museum collections. In addition, our data on individual life histories further illustrate that wild nonhuman primates can survive despite severe dental impairment. The information we provide allows us to comment on questions surrounding the behavior of fossil hominids. Given the relationship between specific food-processing behaviors and patterns of severe wear and tooth loss, these data provide an analogue for reconstructing behavior in the primate fossil record. As data from Beza Mahafaly represent only one location in which ring-tailed lemurs live, it is imperative to test whether the patterns of tooth wear and loss seen at Beza Mahafaly are local phenomena or a species-wide characteristic. Data from other locations and habitats will allow us to fully explore the ideas and explanations presented here.

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