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Temporal Change in Tooth Size Among Ringtailed Lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar: Effects of an Environmental Fluctuation

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20.1. Introduction

Ringtailed lemurs (*Lemur catta*) are among the best-known Malagasy primates (Jolly et al., 2004), with nearly four decades of continuous field research, beginning with Jolly's (1966) seminal work (see Sauther et al., 1999 for a review of ringtailed lemur research). In this way, ringtailed lemurs are comparable to several anthropoid primates, including baboons and chimpanzees, both of which have been intensively studied in the wild since the 1960s (e.g., Altmann, 1980; Goodall, 1986). Despite some notable differences (e.g., Wright, 1999), ringtailed lemurs, in addition to being diurnal, semiterrestrial, and omnivorous, share a number of social attributes with many Old World Monkeys (i.e., living in large, multimale female resident groups; having more than one matriline in each group) (e.g., Hladik, 1975; Sussman, 1992; Sauther et al., 1999). With their long history of study, and their similarities to anthropoid primates, information on ringtailed lemurs is especially important for broad comparisons of primate biology, including hominid paleobiology, as recently seen in discussions of fossil hominid conspecific care (e.g., Lebel and Trinkhaus, 2002; DeGusta, 2003; Cuozzo and Sauther, 2004a, in press).

Among ringtailed lemurs, several populations have been the focus of long-term study (see Sauther et al., 1999 for a review). The ringtailed lemur population at the Beza Mahafaly Special Reserve (BMSR) in southern Madagascar (23°30′S latitude, 44°40′E longitude) is one such group (e.g., Ratsirarson, 1985; Sauther, 1989, 1991, 1992, 1993, 1994, 1998; Sussman, 1991, 1992; Gould, 1996, 1997; Yamashita, 1998, 2000, 2003; Gould et al., 1999, 2003; Sauther et al., 1999, 2001a, 2001b, 2002, this volume; Cuozzo and Sauther, 2004a, 2004b, 2005, in press; see Sussman and Rakotozafy, 1994; Sauther et al., 1999; Gould et al., 1999, 2003; and Ratsirarson, 2003 for detailed descriptions of Beza Mahafaly). Among primates, the population of ringtailed lemurs at BMSR is rare in that detailed dental data (including sets of dental casts) are available from two different points in time (1987/1988 and 2003/2004). This type of information exists for few other primate populations (see Dennis et al., 2004; King et al., 2005; and Lawler et al., 2005 for additional examples). Of special interest, the time interval between the 1987/1988 and 2003/2004 data sets spans a severe drought that occurred in 1991/1992, which resulted in a significant population decline and eventual population rebound among ringtailed lemurs (Gould et al., 1999, 2003). This time interval also spans a nearly complete replacement of this population (Gould et al., 2003; Sauther et al., in preparation).

Recent work on ringtailed lemurs living within the reserve at Beza Mahafaly has produced detailed information on patterns of intraspecific dental variation (Sauther et al., 2001a; Cuozzo et al., 2004), dental health (Sauther et al., 2002; Cuozzo and Sauther, 2004a, 2004b, 2005), and tooth use (Yamashita, 1998, 2003; Cuozzo and Sauther, 2004a, 2004b, 2005). Because of the detailed ecology, life history, and habitat information available for this group of ringtailed lemurs (Sauther et al., 1999), this population provides a rare opportunity to fully explore questions relating to dental variation, dental health, life history, ecology, and evolution. Subsequently, this population also provides an opportunity to investigate examples of microevolution ("allochronic" studies [e.g., Hendry and Kinnison, 1999]) as it relates to short-term, environmental changes such as the drought that severely affected southern Madagascar in 1991 and 1992 (e.g., Sauther, 1998; Gould et al., 1999, 2003; Jolly, 2004).

20.1.1. Research Background

20.1.1.1. Microevolution and Short-term Environmental Perturbation

The term "microevolution" refers to changes within populations or species (Hendry and Kinnison, 1999). Recent studies of micro- or "contemporary" evolution (i.e., observable evolution in heritable traits across a limited number of generations [e.g., Stockwell et al., 2003]) suggest that short-term environmental perturbations (e.g., droughts) can have rapid and measurable effects on living vertebrate populations (see reviews in Hendry and Kinnison, 1999, and Stockwell et al., 2003). The most famous example is from longitudinal studies of the ground finches of the Galápagos Islands (genus *Geospiza*), where research indicates a strong relationship between changes in beak size and drought, with larger beak size being selected as a response to the dominance of harder seeds that remained following the drought (e.g., Grant, 1985; Grant and Grant, 1995). There are numerous other case studies of contemporary evolution, for example those of introduced populations of *Anolis* lizards in the Caribbean (e.g., Losos et al., 2001). Recent reviews of contemporary evolution in response to environmental perturbations among fish, birds, and some mammals, including those of an anthropogenic nature, provide a number of additional examples (Kinnison and Hendry, 2001; Stockwell et al., 2003). Although contemporary evolution resulting from natural selection has been documented among modern humans (see review in Endler, 1986), to our knowledge this has been addressed for few extant nonhuman primates (DeGusta et al., 2003; see review in Endler, 1986).

20.1.1.2. Dental Change Over Time

Studies of dental change over time are important for a number of questions in evolutionary biology. Because mammalian tooth size is highly heritable (e.g., Gingerich, 1974b; Hillson, 1986; Hlusko et al., 2002) and crown size does not change after tooth formation (e.g., Swindler, 2002; DeGusta et al., 2003) except by attrition or pathology (e.g., Perzigian, 1975; DeGusta et al., 2003), changes in tooth size in the fossil record of primates and other mammals have successfully been used to address questions of phylogeny, adaptation, and climate change (e.g., Gingerich, 1974a, 1979a, 1979b, 1985, 1994; Gingerich and Schoeninger, 1977; Bown et al., 1994; Cuozzo, 2002). For example, among early Eocene mammals (e.g., the condylarthran genus *Hyopsodus*), changes in tooth size show a strong correlation with temperature fluctuations and their corresponding biostratigraphic units (e.g., Gingerich, 1974a; Bown et al., 1994; Cuozzo, 2002). This suggests that mammalian tooth size can reflect biological responses (e.g., an increase in body size) to a changing environment over time. Also, several studies (e.g., Kurten, 1957; Van Valen, 1963; Marcus, 1969) have used changes in tooth size across age cohorts in assemblages of fossil mammals (including primates) to document examples of natural selection. However, there are few empirical studies that demonstrate microevolution for dental characteristics in extant mammals (see review in Endler, 1986). One of the few examples comes from work on several modern human populations, where selection for larger tooth size occurred in response to intense tooth wear and severe crown attrition (Greene et al., 1967; Perzigian, 1975). In addition, a recent study of tooth size in an extant howler monkey population (*Alouatta palliata*) demonstrated that individuals with smaller molars had significantly decreased fitness, thereby suggesting selection for larger teeth (DeGusta et al., 2003). Given its high heritability, investigating possible changes in tooth size in a single population of primates—especially when the temporal interval spans a severe environmental change (i.e., drought)—allows us to explore the impact, and possible selective pressure (i.e., directional selection) of ecological changes and subsequent behavioral modifications (i.e., increased competition and/or aggression) on contemporary evolution.

20.1.1.3. Drought and Patterns of Mortality at Beza Mahafaly Special Reserve

Southern Madagascar underwent a severe drought in the early 1990s (e.g., Sauther, 1998; Gould et al., 1999, 2003) that, among other results, led to a widespread human famine (Jolly, 2004). During and following this drought, the ringtailed lemurs at Beza Mahafaly experienced a significant population decline, with the adult population dropping from 85 individuals in early 1991 to 51 in 1994 (Gould et al., 1999). By 2001, the adult population (n = 61) had recovered to near that of 1987 (n = 65), although still below that of the pre-drought peak in 1991 (Gould et al., 2003). In addition, as of 2001, this population had undergone nearly a complete replacement since 1987 (Gould et al., 2003; Sauther et al., in preparation). This drought had a particularly severe impact on adult females, infants, and juveniles (when compared with predrought years), with 21% of all adult females, 80% of all infants, and 57% of juveniles in three focal groups, having died during the 6 months from September 1992 through March 1993 (Gould et al., 1999). In addition, female mortality increased to 29% in 1993/1994, the year following the drought (Gould et al., 1999). Also of note, all females that died in 1992/93 had infants and were lactating (Gould et al., 1999).

20.1.1.4. Enamel Thickness, the Drought, and Food Availability

Despite this species possessing among the most thin enamel of all extant primates (e.g., Shellis, 1998; Martin et al., 2003; Godfrey et al., 2005), ringtailed lemurs living in and around areas of gallery forest across southern Madagascar have a diet dominated by tough, hard fruit of the tamarind tree, *Tamarindus indica* (e.g., Jolly, 1966; Sauther, 1998; Yamashita, 2000, 2003, in preparation; Simmen et al., this volume). Although not a perfect relationship (e.g., Martin et al., 2003), primate enamel thickness generally exhibits a strong correspondence with diet (e.g., Shellis et al., 1998). *T. indica* reproduces asynchronously (Sauther, 1998). Tamarind fruit is therefore available year round, hence being a ringtailed lemur keystone food source (Jolly, 1966; Sauther, 1998; Sauther et al., 2002; Cuozzo and Sauther 2004a; Simmen et al., this volume). In addition, during the dry season, tamarind is the primary food used at Beza Mahafaly (Sauther, 1998; Simmen et al., this volume). Tamarind fruit is also larger than all other foods used by the Beza Mahafaly ringtailed lemurs (e.g., Sauther, 1992), and thereby presents a very challenging food source (Figures 20.1a, 20.1b, and 20.2; see also Figure 8.1 in Mertl-Millhollen et al., this volume).

Ringtailed lemurs primarily process tamarind pods with their postcanine teeth (e.g., Sauther et al., 2002; Yamashita, 2003; Cuozzo and Sauther, 2004a, 2004b, 2005, in press), and it is this region of the mouth where severe attrition and tooth loss most often occur (e.g., Cuozzo and Sauther, 2004a, 2004b, 2005, in press). Although hard tamarind seeds are passed through the digestive system primarily unscathed (e.g., Yamashita, 2000; Simmen et al., this volume), accessing these seeds takes a severe toll on ringtailed lemur teeth. The outer casing of ripe tamarind pods is both hard and tough, in fact the hardest and toughest of all foods

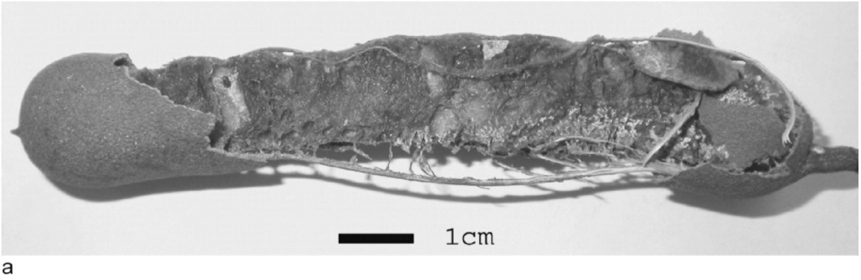

FIGURE 20.1. (a) A tamarind pod (*Tamarindus indica*) from Beza Mahafaly, with outer casing intentionally removed to show enclosed fruit (scale bar = 1 cm).

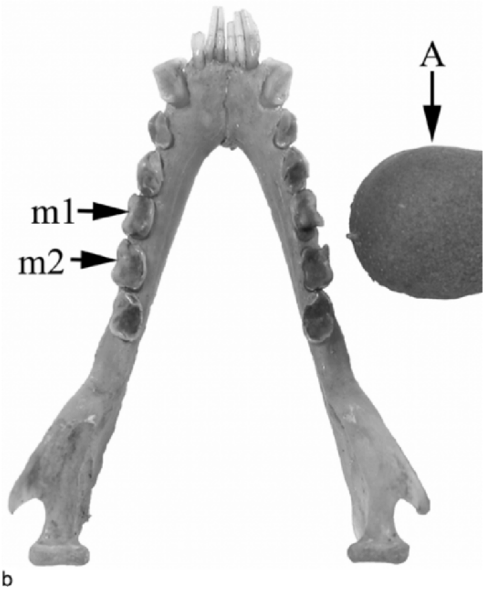

FIGURE 20.1. (*Continued*) (b) Illustration of the size of a tamarind pod (A) relative to tooth and mandible size in a ringtailed lemur skeletal specimen (BMOC 67).

consumed by ringtailed lemurs (Yamashita, 2000, in preparation; Cuozzo and Sauther, in press). When processing these pods, the outer casing is initially broken open in the region of the first and second molars, as well as the adjacent premolars, with the pod often being bitten down upon several times in order to initiate crack formation (Cuozzo and Sauther, 2005, in press). In addition, extraction of the seeds from the pod requires additional tooth use, with the hard, tough outer casing of the pod and the tough internal fibers (Figures 20.1a and 20.2) continually making contact with the surface of the teeth (Cuozzo and Sauther, 2004b, 2005, in press). Although tooth wear is a complex process resulting from the interaction of numerous variables (e.g., Maas and Dumont, 1999), the excessive amount of tooth wear and subsequent tooth loss seen among the ringtailed lemurs at Beza Mahafaly (Figures 20.3, 20.4, 20.5a, and 20.5b) is largely caused by processing the hard, tough pods of the tamarind tree (Cuozzo and Sauther, 2004a, 2004b, 2005, in press).

Despite the large size of tamarind pods (Figures 20.1a, 20.1b, and 20.2), ringtailed lemurs have very small maxillary first molars (relative to skull and palate length) when compared to other living and extinct lemurs (Godfrey et al., 2002). Therefore, ringtailed lemurs have molars with a small food processing area relative to the size of their keystone food (Figure 20.1b). When combined with thin enamel, early relative first molar eruption among lemurids (e.g., Eaglen, 1985; Godfrey et al., 2001, 2004), and a diet dominated by a hard, tough keystone food

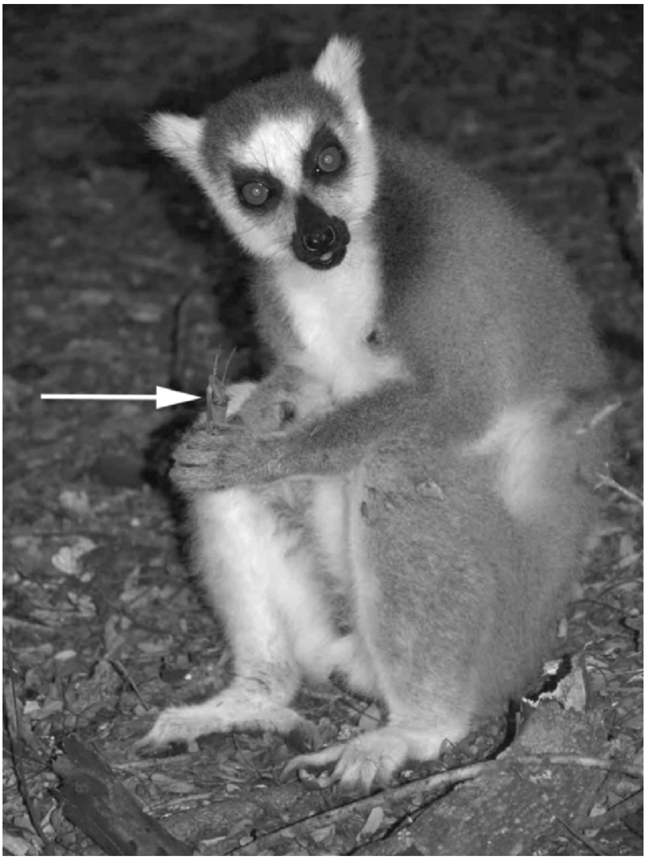

FIGURE 20.2. A partially processed tamarind pod (white arrow) being held by a ringtailed lemur. Note the relative size of this partial pod, as well as the tough internal fibers that remain after initial processing. Photo, Michelle Sauther.

(tamarind fruit), the small size of the first molars (with a small food processing area and limited enamel surface) likely contributes to their high frequency of severe wear (see Figures 20.3, 20.4, 20.5a, and 20.5b) and eventual antemortem loss (Cuozzo and Sauther, 2004a, 2004b, 2005, in press). Given the large size of tamarind pods relative to the size of ringtailed lemur mouths and teeth (see Figures 20.1b and 20.2), larger molars—with a larger surface area and increased processing platform—would be beneficial during mastication (e.g., Perzigian, 1975). As discussed by Janis and Fortelius (1988) and Lucas (2004), increased tooth size is one way (along with increased enamel thickness) to increase the functional longevity of teeth. With the intense nutritional stress due to resource scarcity during the drought, the ability to effectively process this limited food resource could be a selective factor. Hence, we tested for changes in dental size.

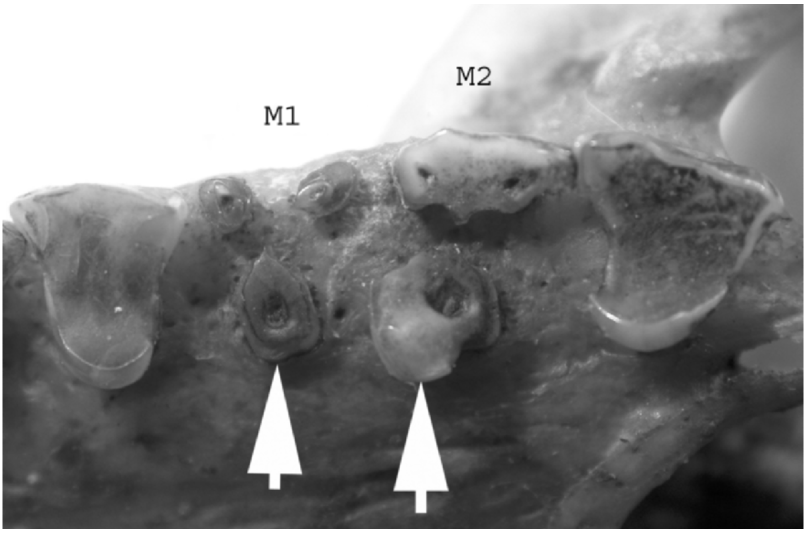

FIGURE 20.3. Tooth wear in a ringtailed lemur skeletal specimen from the Beza Mahafaly Osteological Collection (BMOC 67). Note the extensive wear and damage to M1 and M2, with white arrows marking the remaining lingual areas of the tooth crowns.

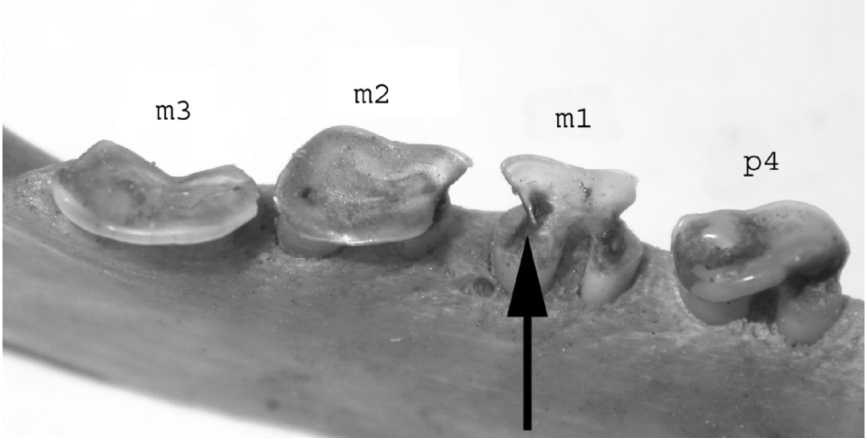

FIGURE 20.4. Tooth wear in a ringtailed lemur skeletal specimen from the Beza Mahafaly Osteological Collection (BMOC 70). Note the extensive wear and damage to m1, with black arrow marking the damaged lingual portion of the crown.

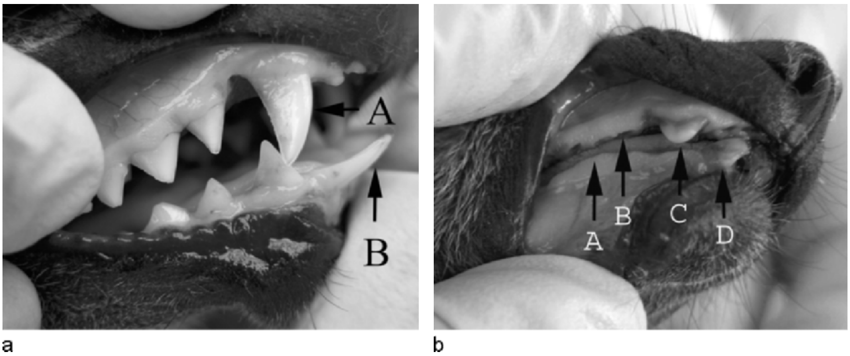

FIGURE 20.5. (a) Unworn teeth in a living 3-year-old ringtailed lemur (Yellow 187). A, Unworn right maxillary canine. B, Unworn right mandibular canine (toothcomb). (b) Severe wear and tooth loss in a living ringtailed lemur (Blue 132). A, Right mandibular gumline with no teeth present. B, Right maxillary P2 worn to the gumline, with only worn roots remaining. C, Heavily worn right maxillary canine. D, Worn right mandibular canine (toothcomb).

20.1.2. Research Questions

As seen in Hendry's (2005) recent discussion of the power of natural selection, determining the strength of natural selection can be elusive (see Lawler et al., 2005 for a study of the strength of selection in an extant primate population). Therefore, our primary goal in this study is to investigate the possible role of a severe drought as a selective pressure within a living population of ringtailed lemurs. Here we compare tooth size between the 1987/1988 and 2003/2004 Beza Mahafaly ringtailed lemur samples in order to address the following questions:

1. Did particular tooth positions exhibit a size increase in the reserve population between 1987/1988 and 2003/2004, following the drought? If so, what ecological, behavioral, and/or mechanical factors would lead to changes in tooth size following the drought?
2. Did specific tooth positions experience a size increase in either males or females selectively between 1987/1988 and 2003/2004, following the drought?

Answers to these questions provide a baseline for future work, as the ringtailed lemur population at Beza Mahafaly is currently the focus of a longitudinal study of ecology and dental life history (e.g., Cuozzo and Sauther, 2004a, 2004b, 2005, in press; Sauther et al., in preparation). In addition, this project provides a direct investigation of the role of ecological change as a selective force in mammalian evolution, which is less common in studies of contemporary evolution, as seen in Endler's (1986) compilation of studies of natural selection in wild populations (see summaries of more recent work in Hendry and Kinnison, 1999, and Stockwell et al., 2003).

20.2. Materials and Methods

In 1987/1988 and 2003/2004, dental data, including complete sets of dental impressions, were collected from sedated lemurs at Beza Mahafaly. Methods of impression collection and cast production for the 1987/1988 data have previously been described in detail (Sauther et al., 2001a). For the 2003/2004 sample, impressions were made using custom-built impression trays and Presidents Jet Regular Body polyvinalsiloxane impression material. Casts were made from Coecal™ Type III dental stone, similar to the dental stone used in 1987/1988 (Sauther et al., 2001a). The sample size from 1987/1988 includes 45 individuals, with 39 adults; the 2003/2004 sample consists of 83 adults among the 92 individuals captured and studied. No lemurs from 2003/2004 had dental data collected in 1987/1988 as only one individual included among the 2003/2004 data was alive (as a subadult) in 1987/1988 (Sauther and Cuozzo unpublished data).

Metric data were collected from the casts of both data sets using Fowler digital needle-point calipers measured to the nearest 0.01 mm. The one exception is toothcomb breadth from 2003/2004, which was collected from sedated lemurs in the field, using dial calipers measured to the nearest 0.05 mm. The same individual (F.C.) collected all measurements, thereby eliminating the potential for interobserver error. Due to variations in cast quality and individual dental pathology (e.g., dental abscesses, tooth wear, tooth loss) sample sizes vary for each variable. Measurements collected include (1) maxillary toothrow length (measured from the anterior margin of the canine to the distal border of M^3), (2) mandibular toothrow length (measured from the anterior margin of P_2 [the mandibular canine in *Lemur catta* is part of the toothcomb, as in most strepsirrhine primates] to the distal border of M_3), (3) palate breadth (measured from the lateral borders of M^3), (4) toothcomb breadth (measured from the lateral borders of the mandibular canines), (5) P_2 length (measured mesiodistally at the base of the tooth), (6) lengths of M^1 and M^2 (the maximum mesiodistal length measured across the lingual cusps), and (7) lengths of M_1 and M_2 (measured mesiodistally from the anterior margin of the trigonid to the distal border of the talonid). Mesiodistal tooth lengths were selected as indicators of overall tooth size due to their limited metric variability when compared to buccolingual width in this population of lemurs (Sauther et al., 2001), as well as in mammals in general (e.g., Gingerich, 1974b).

As crown size does not change after tooth formation (e.g., Swindler, 2002), except as a result of attrition or pathology (e.g., Perzigian, 1975; DeGusta et al., 2003), measurements from the permanent teeth present in subadults (maxillary and mandibular first and second molar lengths, and toothcomb breadth) are included in the data set. The presence of either deciduous or partially erupted adult maxillary canines (as well as adult P_2) affects toothrow length. Hence, this measure was not collected for subadults. Metric data for the two overall temporal samples were compared in order to test whether any measures increased following the drought. Sex-specific metric data were also compared between 1987/1988 and 2003/2004, in order to test whether males or females exhibited a change in tooth size across the temporal interval. We investigated directional change in lengths of the first and second maxillary and mandibular molars (which are central in processing tamarind pods), toothrow length (which is in part a product of tooth size), toothcomb breadth (as toothcombs are used in food acquisition [e.g., Sauther et al., 2002; Yamashita, 2003]), and caniniform P_2 (which is involved in food acquisition [e.g., Sauther et al., 2002] and sometimes food processing). In order to evaluate whether changes in tooth size were a function of change in overall cranial size, we also examined size change in palate breadth (measured at M^3), as this measure provides a strong indicator of skull width (and therefore skull size). All comparisons were tested for significant differences using unpaired student's t-tests ($p = 0.05$), and were conducted using Statview statistical and data analysis software (Haycock et al., 1992).

Following standards outlined by the U.S. CITES Management Authority (a unit of the U.S. Fish and Wildlife Service), as well as the Institutional Animal Care and Use Committee (IACUC) of the University of Colorado, each member of the research team wore protective covering such as surgical masks and gloves during initial data collection, in order to preclude disease transfer while handling lemurs. Furthermore, all methods and materials received approval by and followed standard animal handling guidelines (University of Colorado IACUC).

20.3. Results

Metric data for the 1987/1988 and 2003/2004 overall samples are compared in Table 20.1, and sex-specific temporal comparisons are presented in Tables 20.2 and 20.3. Of the nine variables studied, significant ($p < 0.01$) increases occurred in P_2, M_1, and M_2 length in the overall population. Somewhat unexpectedly, M^2 showed a significant ($p = 0.0325$) decrease in length between 1987/1988 and 2003/2004 in the population. Among males, as in the overall sample, M_1 and M_2 length showed significant ($p < 0.05$) increases. However, in contrast to the overall population, neither P_2 nor M^2 length ($p > 0.10$) displayed a significant change in size. Females exhibited a pattern similar to the overall and male samples, with a significant ($p = 0.0158$) increase in the length of M_2. Females, in congruence with the overall sample, experienced a significant ($p = 0.0248$) increase in P_2 length. In contrast, neither M_1 length (although larger in 2003/04 than 1987/88 [$p = 0.2009$] as with both the overall and male samples) nor M^2 length (shorter in 2003/2004 [$p = 0.0673$] as in the overall sample) exhibited a significant change. Palate breadth did not exhibit a significant temporal size change in either the overall population ($p = 0.6864$), or in the sex-specific samples (males, $p = 0.2178$;

TABLE 20.1. Ringtailed lemur tooth size compared between 1987/1988 and 2003/2004.

Variable	1987/1988[a]				2003/2004[d]				
	n	Mean[b]	STD	CV[c]	n	Mean[b]	STD	CV[c]	p value[e]
Maxillary toothrow length	23	35.13	0.94	2.70	42	35.20	0.96	2.70	0.7763
Mandibular toothrow length	21	31.07	0.62	2.00	47	30.74	0.79	2.60	0.0935
Palate breadth at M^3	21	26.28	0.77	2.90	32	26.20	0.65	2.50	0.6864
P$_2$ length	16	4.64	0.20	4.20	42	**4.86**	0.24	4.90	**0.0081**
Toothcomb breadth	20	7.26	0.25	3.40	81	7.15	0.28	4.00	0.1130
M^1 length	27	4.87	0.23	4.80	37	4.88	0.19	3.90	0.9393
M$_1$ length	22	5.04	0.18	3.60	34	**5.19**	0.20	3.90	**0.0071**
M^2 length	26	**5.26**	0.23	4.30	39	5.16	0.13	2.50	**0.0325**
M$_2$ length	26	5.39	0.22	4.00	45	**5.57**	0.16	2.90	**0.0002**

[a] Values presented for 1987/1988 differ slightly from those published in Table 3 of Sauther et al. (2001a) for this population due to the addition of data from (1) several adults and (2) the permanent teeth of non-adults, not previously included.

[b] All means in mm.

[c] CV = standard deviation ÷ mean × 100.

[d] Boldfaced values indicate a significantly different mean ($p < 0.05$).

[e] p value for t-tests of means between 1987/1988 and 2003/2004.

TABLE 20.2. Ringtailed lemur tooth size compared for males between 1987/1988 and 2003/2004.

Variable	1987/1988[a]				2003/2004[d]				
	n	Mean[b]	STD	CV[c]	n	Mean[b]	STD	CV[c]	p value[e]
Maxillary toothrow length	13	35.03	1.11	3.20	22	35.36	0.99	2.80	0.3690
Mandibular toothrow length	13	31.14	0.66	2.10	23	30.92	0.73	2.40	0.3955
Palate breadth at M^3	12	26.50	0.71	2.70	18	26.16	0.72	2.80	0.2178
P$_2$ length	10	4.72	0.21	4.50	21	4.87	0.25	5.20	0.1025
Toothcomb breadth	10	7.26	0.17	2.40	39	7.12	0.28	3.90	0.1459
M^1 length	11	4.83	0.21	4.20	16	4.86	0.21	4.40	0.6329
M$_1$ length	11	5.00	0.20	4.00	13	**5.21**	0.23	4.30	**0.0211**
M^2 length	14	5.22	0.25	4.70	19	5.14	0.12	2.30	0.2029
M$_2$ length	14	5.37	0.20	3.70	21	**5.56**	0.18	3.30	**0.0082**

[a] Values presented for 1987/1988 differ slightly from those published in Table 3 of Sauther et al. (2001a) for this population due to the addition of data from (1) several adults and (2) the permanent teeth of non-adults, not previously included.

[b] All means in mm.

[c] CV = standard deviation ÷ mean × 100.

[d] Boldfaced values indicate a significantly different ($p < 0.05$).

[e] p value for t-tests for means between 1987/1988 and 2003/2004.

TABLE 20.3. Ringtailed lemur tooth size compared for females between 1987/1988 and 2003/2004.

	1987/1988[a]				2003/2004[d]				
Variable	n	Mean[b]	STD	CV[c]	n	Mean[b]	STD	CV[c]	p value[e]
Maxillary toothrow length	10	35.26	0.72	2.00	20	35.02	0.91	2.60	0.4851
Mandibular toothrow length	8	30.98	0.59	1.90	24	30.57	0.82	2.70	0.2061
Palate breadth at M^3	9	25.99	0.79	3.00	14	26.25	0.58	2.20	0.3665
P_2 length	6	4.61	0.16	3.60	21	**4.84**	0.23	4.70	**0.0248**
Toothcomb breadth	10	7.24	0.31	4.30	42	7.19	0.29	4.00	0.4046
M^1 length	16	4.91	0.25	5.10	21	4.89	0.17	3.50	0.7800
M_1 length	11	5.09	0.16	3.20	21	5.18	0.19	3.70	0.2009
M^2 length	12	5.29	0.20	3.80	20	5.18	0.14	2.70	0.0673
M_2 length	12	5.42	0.24	4.40	24	**5.58**	0.15	2.60	**0.0158**

[a] Values presented for 1987/1988 differ slightly from those published in Table 3 of Sauther et al. (2001a) for this population due to the addition of data from (1) several adults and (2) the permanent teeth of non-adults, not previously included.

[b] All means in mm.

[c] CV = standard deviation ÷ mean × 100.

[d] Boldfaced values indicate a significantly different mean ($p < 0.05$).

[e] p value for t-tests for means between 1987/1988 and 2003/2004.

females $p = 0.2178$). This indicates that changes in tooth size were not a function of overall skull size change.

20.4. Discussion

20.4.1. Ontogeny, Weaning, and Increased Tooth Size

What factors would lead to increased tooth size in this population after a drought? Eaglen (1985) and Godfrey et al. (2001) discussed the role of natural selection as it relates to dental development, weaning, and ecology, specifically in terms of lemur biology and evolution. Ringtailed lemurs exhibit a pattern of rapid growth and development, with dramatic increases in body mass occurring during the first seven months of life (e.g., Pereira, 1993). This pattern of growth accelerates in the fourth month (Pereira, 1993), which roughly corresponds with both eruption of the adult first molars and weaning (e.g., Eaglen, 1985; Godfrey et al., 2001). Therefore, M_1 is important for the transition to an adult diet (as is true for primates in general [e.g., Godfrey et al., 2001]). As M_2 erupts in month seven (Eaglen, 1985), each of the two molar positions (M_1 and M_2) that experienced a size increase in the Beza Mahafaly ringtailed lemur population are present during the period of rapid development and body mass increase described by Pereira (1993). Of importance for our discussion, this period of rapid growth and development corresponds to the time during 1992/1993 when infants experienced 80% mortality (Gould et al., 1999). Given the high mortality of infants at this time (only six of 30 infants survived [Gould et al., 1999]), any trait that produced an advantage when processing keystone foods would have aided survival during this period. We argue that larger molars would be such a trait. Considering that notable wear of adult M_1 is present in subadults, and that marked wear is observable on deciduous teeth (e.g., Cuozzo and Sauther, 2004a, 2005, in press), the importance of larger permanent first and second mandibular molars becomes apparent (see Janis and Fortelius, 1988; Lucas, 2004). The amount of wear on subadult and deciduous teeth also indicates the importance of processing adult foods (dominated by tamarind fruit) by juveniles. As juveniles also experienced high mortality (57%) during late 1992 and early 1993 (Gould et al., 1999), larger teeth would have contributed to their likelihood of survival during this period of intense resource stress. Because infants and juveniles would not only have been competing for resources with members of their cohorts, but also with adults, any slight advantage in processing fallback foods (such as larger teeth) would have been especially beneficial at a time when younger individuals are under tremendous nutritional pressure.

20.4.2. Socioecology and Increased Tooth Size

As outlined earlier, larger teeth would provide a food processing advantage for ringtailed lemurs, given the dominance of a relatively large, tough, and hard keystone food. However, the mechanical advantage of larger teeth during the drought years would also have been enhanced by ringtailed lemur socioecology. Sauther (1993) noted that ringtailed lemurs are under continual feeding stress throughout the year. As conditions during the drought severely affected this population, as seen in increased mortality (with at least one entire troop disappearing [Gould et al., 1999]) and increased exploitation of poor quality foods (e.g., Sauther, 1998; Gould et al., 1999, 2003), resource competition was likely exaggerated, thereby leading to an increase in interindividual competition for resources. As Sauther (1993) reported, agonism among ringtailed lemurs often consists of aggressive agonism surrounding resource competition. Wright (1999), in a review of the effects of drought on lemurs, noted that increased aggression and resource competition occurred among lemurs in the dry forests of southern Madagascar. This was also noted by Jolly et al. (1993) at Berenty Reserve in southeastern Madagascar, where within-group competition and displacement of lower ranking female ringtailed lemurs increased during the 1991/1992 drought. During a period of resource reduction and scarcity, products of the tamarind tree, as the primary food source, would likely have become emphasized (see Lambert et al., 2004 for a recent discussion of the role of fallback foods in primate dental evolution). As females have first choice of food (male displacement of females is rare [Sauther, 1993]), males are often left to feed on poorer quality foods, such as leaves, during the dry season when food resources are limited (Sauther, 1994; Sauther et al., 2002). This suggests that larger food processing teeth would be advantageous for males, when viewed in the socioecological context of female dominance during a time of resource limitations. Although male mortality rates are not available due to continual male migration (Gould et al., 1999), it is likely that adult males, similar to adult females, infants, and juveniles, experienced increased mortality resulting from the drought (Gould et al., 1999).

However, the advantage that larger teeth would provide is not limited to males. The reproductive pattern of ringtailed lemurs, like many other Malagasy primates (e.g., Wright, 1999), is linked to resource availability, with different stages of the reproductive cycle (i.e., mating, gestation, birth, lactation) showing a strong correspondence to availability of specific food sources (Sauther, 1998). Ringtailed lemurs, similar to other Malagasy primates (e.g., Wright, 1999), exhibit reproductive synchrony, with females at Beza Mahafaly usually giving birth in October/November (e.g., Sauther, 1998; Sauther et al., 1999). Female ringtailed lemurs are pregnant during the dry months of the austral winter, when food resources are limited (e.g., Sauther, 1998), and hence give birth and begin lactation with little or no nutrient reserves (Sauther, 1998). Although several foods are available periodically, the primary food consumed during these times of nutritional stress is tamarind fruit (e.g., Sauther, 1998; Simmen et al., this volume). This situation was likely exacerbated during the drought of 1991/1992 (Sauther, 1998). In a time of resource scarcity, larger teeth, and an improved ability to process keystone and/or fallback foods, would benefit females who, despite having feeding priority, were under tremendous nutritional stress during gestation and lactation. As females experienced very high mortality during and following the drought (21% in 1992/1993; 29% in 1993/1994) at Beza Mahafaly (e.g., Gould et al., 1999), especially among lactating females with infants, the nutritional pressure on females would have been exaggerated. Although a number of foods are available during the various stages of the reproductive cycle, only tamarind is available for long periods and throughout the year (Sauther, 1998; Simmen et al., this volume). In this context, even slight advantages, whether physical (e.g., larger teeth for processing tamarind fruit) or behavioral (e.g., dominance rank), likely played a key role in determining which individuals survived the drought, and which would successfully reproduce (Sauther et al., in preparation).

Although our primary goal in this study was to investigate the possible selective pressure of a severe drought, rather than address the power of selection, we have computed values for selection intensity in order to place our data in a broader context. Selection intensity (see discussions in Endler, 1986 and Futuyma, 1998), also known as the directional selection differential (e.g., Grant, 1985), is a value that compares the intensity of quantitative change in terms of standard deviations. In our sample, the values for selection intensity (i) for M_1 length ($i = 0.71$) and M_2 length ($i = 0.90$) indicate that these traits increased by close to one full standard deviation. In his review of estimates of selection intensity, Endler (1986) noted that studies indicating intense selection exhibited values for i ranging from one half to sometimes two full standard deviations (see review in Futuyma, 1998). These data indicate that selection for increased M_1 and M_2 length in our study is comparable to a number of other previous studies. Thus, it appears that directional selection for larger teeth has occurred at a number of tooth positions in this population of lemurs, affecting both males and females (albeit caused by different yet compounding selective pressures) with an ecological perturbation (i.e., drought) being a primary catalyst.

20.4.3. Increased Tooth Size in a High-Attrition Environment

Mammalian teeth provide a faithful record of an individual's growth and development, evolutionary relationships, and life story (e.g., Morbeck, 1997; Schwartz and Dean, 2000). Previous data on the patterns of tooth use, wear, and eventual loss in this population illustrate that *L. catta* teeth directly reflect their interaction with the environment of Beza Mahafaly (e.g., Sauther et al., 2002; Cuozzo and Sauther, 2004a, 2004b, 2005). This population of ringtailed lemurs is notable for their high frequency of severe wear and tooth loss (Sauther et al., 2002; Cuozzo and Sauther, 2004a, 2004b, 2005, in press; see Figures 20.3, 20.4, and 20.5b). This pattern contrasts with sympatric *Propithecus verreauxi*, which exhibits far less wear and few missing teeth (Cuozzo and Sauther, in press). Excessive tooth wear has also been observed among the ringtailed lemurs at Berenty Reserve in southeastern Madagascar (Soma, pers. comm.; Crawford, pers. comm.) where, similar to Beza Mahafaly, tamarind provides a keystone food source (e.g., Jolly, 1966; Simmen et al., this volume). Perzigian (1975), in a study of natural selection in a historic population of modern humans, argued that larger teeth would be advantageous, and therefore "of some survival value especially where attrition is very pronounced." Greene et al. (1967) came to a similar conclusion for a Mesolithic human population. Lucas (2004) has also discussed increased tooth size as one possible response to continued wear. In contrast to other primate populations, as well as sympatric Verreaux's sifaka (Cuozzo and Sauther, in press), in which tooth loss is often a product of tooth damage and disease (e.g., Schultz, 1935; Smith et al., 1977; Lovell, 1990), tooth loss among the Beza Mahafaly ringtailed lemurs is primarily a product of excessive wear (e.g., Cuozzo and Sauther, 2004a, 2004b, 2005, in press). Among these ringtailed lemurs, M_1 begins to wear shortly after eruption, is usually the first tooth lost, and is the most frequently missing tooth in the population (Cuozzo and Sauther, 2004a, 2005, in press). In a population where M_1 is often severely worn and frequently absent, M_2 (even when worn) becomes especially important for mastication, as it often remains functioning long after M_1 (as well as P_3 and P_4) is lost (Cuozzo and Sauther, 2005, in press). In this context, larger first and second molars would be quite advantageous.

A similar argument can also be made for increased size in P_2. Ringtailed lemurs primarily process tamarind pods with their postcanine teeth (e.g., Sauther et al., 2002; Yamashita, 2003; Cuozzo and Sauther, 2004a, 2005, in press). However, the anterior teeth (e.g., P_2) are often used in the initial acquisition of this food (e.g., Sauther et al., 2002). In individuals with severe tooth wear and antemortem tooth loss, anterior teeth become important for food processing. This is seen in the individual lemur shown in Figure 20.5b, in which the maxillary canine is clearly worn (the end of the tooth is short, and quite rounded, indicating wear rather than breakage), and is not uncommon in this population. Among tooth positions, P_2 is among the least frequently missing teeth in ringtailed lemurs, although sometimes being severely worn (Cuozzo and Sauther, 2004a, 2005, in press). Therefore, a larger P_2 (even if damaged) would provide an extended surface for food processing in individuals whose postcanine teeth have been severely impaired, as often seen at Beza Mahafaly (Sauther et al., 2002, Cuozzo and Sauther, 2004a, 2004b, 2005, in press).

Selection for larger (and possibly longer lasting) teeth in a high attrition environment primarily relates to long-term survival, rather than to the effects of a severe but short-lived event such as the drought of 1991/1992. However, given the high frequency of excessive tooth wear in this population (e.g., Sauther et al., 2001a, 2002; Cuozzo and Sauther, 2004a, 2004b, 2005, in press)—which indicates the importance of tamarind fruit—the scenario described by Greene et al. (1967) and Perzigian (1975) among modern human populations provides an important context with which to understand the possible selective pressure of diet on dental evolution. Given this scenario, we might expect that rapid and excessive tooth wear in ringtailed lemurs could lead to selection for larger food processing teeth, as discussed by Lucas (2004). This becomes more likely when viewed in context of the intense nutritional and reproductive stress experienced by ringtailed lemurs during and following the drought of 1991/1992. This high attrition environment provides a constant pressure in this population of ringtailed lemurs, and the added stress resulting from the drought likely exacerbated this pressure. As our long-term research plans at Beza Mahafaly include the continued collection of longitudinal dental data (at both the individual and populations levels), we will be able to further explore the relationship between tooth wear and possible changes in tooth size, including studies of tooth size across a temporal span that is not affected by severe drought.

20.4.4. M^2 Size Reduction: Selection for Improved Occlusion?

Having provided explanatory scenarios for increased tooth size in this population, we must now address the unexpected decrease in M^2 length. Contrary to our expectations, M^2 experienced a significant ($p = 0.0325$) length decrease in the overall sample since 1987/1988. The pattern of simultaneous size increases in some tooth positions with size decreases in others is not without precedent. Both Kurten (1957), in a study of tooth size change in the European cave bear (*Ursus spelaeus*), and Van Valen (1963) in the Miocene horse *Mercyhippus primus*, documented this type of apparent conflict. Van Valen (1963), in discussing the simultaneous trends of smaller maxillary teeth yet larger mandibular teeth in *M. primus*, suggested that the decrease in maxillary tooth size might have represented a local or temporary reversal, as this species was increasing in overall size. Kurten (1957), when analyzing size changes in molar cusps, noted that cave bear

M^2 paracones became smaller, while the corresponding "valley" areas of M_2 became larger. This apparent paradox likely resulted from selection on the masticatory functional complex resulting from occlusion between the two teeth, with the two size trends leading to more efficient occlusion. The trend seen in our current data may reflect a similar pattern of selection, as the morphology of ringtailed lemur molars reflects their functional occlusion (e.g., Yamashita, 1998). *L. catta* M_2 basins are quite deep relative to other lemurids and may function as food retainers in which the breakdown of food is enhanced (Yamashita, 1998). Yamashita (1998) also noted that ringtailed lemur second molars have long crests with acute cusps, and that there is a "loose fit" between the M_2 hypoconid and M^2 trigon. It is possible that the increase in M_2 length accompanied by a decrease in M^2 length documented in our data reflects the type of functional selection postulated by Kurten (1957), given the function of ringtailed lemur second molar morphology discussed by Yamashita (1998). It is also interesting that the amount of variation in M^2 length (compare standard deviations for 1987/1988 and 2003/2004 in Table 20.1) significantly decreased (F ratio [variance], $p = 0.0043$), suggesting directional selection not only for size, but also for a reduction in variability (i.e., possibly targeting a "tighter" metric distribution and greater occlusal efficiency). Because the types of morphometric data collected by Kurten (1957) and Yamashita (1998) are accessible in the dental casts used in our study from both 1987/1988 and 2003/2004, we plan to further investigate this hypothesis as part of our continued research.

One other possible explanation for the reduction in M^2 length in this population was discussed by Brace et al. (1987), in which dental reduction in modern humans, albeit over a much longer period of time, resulted from the "Probable Mutation Effect" (Brace, 1963). In this scenario, reductions in tooth size may be caused by mutation alone, given an absence of natural selection (i.e., relaxed selection) (Brace et al., 1987). It is therefore possible that directional selection did not impact the maxillary teeth.

20.5. Conclusions

In a broad discussion and review of lemur ecology and evolution, Wright (1999) posed the question "What effect does drought have on a tropical fauna?" Wright (1999) argued that many of the characteristics unique to the Malagasy strepsirrhines (e.g., female dominance, reproductive synchrony) evolved in response to the challenges of Madagascar's unpredictable environment, for example seasonal fluctuations, cyclones, and droughts. Given the strong link between lemur biology, ecology, behavior, and the environment, investigating the response of lemurs to environmental changes in the wild, especially among populations for which longitudinal data are available, provides the opportunity to document examples of contemporary evolution. As noted earlier, the drought of 1991/1992 had a major impact on southern Madagascar (e.g., Sauther, 1998; Gould et al., 1999, 2003; Jolly, 2004). The ringtailed lemurs at Beza Mahafaly are no exception, as witnessed by a significant decrease in the adult population, and dramatic increases in adult female, infant and juvenile mortality in the years during and following the drought (Gould et al., 1999, 2003). This population also experienced a change in its dental characteristics, as P_2, M_1, and M_2 lengths each significantly increased ($p < 0.01$) in the overall population between 1987/1988 and 2003/2004.

Studies of tooth size change over time provide an opportunity to explore a number of questions in primate evolution and evolutionary biology (see earlier references). Our data, from a living population of ringtailed lemurs, have allowed us to conduct an allochronic study of primate dental size, and to investigate the impact of a severe drought on the contemporary evolution of this population. Because mammalian tooth size is highly heritable (e.g., Gingerich, 1974b; Hillson, 1986; Hlusko et al., 2002), these data indicate that environmental fluctuations (e.g., drought), combined with the use of a challenging keystone food, can provide important selective pressures on the evolution of primate teeth (as recently suggested by Lambert et al., 2004 in the evolution of primate enamel thickness), and more broadly, can lead to observable changes in a population in contemporary time. These data correspond to other studies of contemporary evolution in vertebrate populations (e.g., Galápagos finches), and illustrate the effect that rapid ecological changes can have on living populations (e.g., Grant and Grant, 1995; see reviews in Hendry and Kinnison, 1999, and Stockwell et al., 2003). In addition, our results indicate that socioecology (e.g., resource competition, interindividual aggression) can be an important variable when investigating natural selection, environmental change, and contemporary evolution. Although it is not possible to completely rule out genetic drift (e.g., immigration of larger-toothed individuals) as a cause of the increased tooth size seen in this population, it is unlikely. New data on male migration (females do not usually migrate [e.g., Sussman, 1992]) indicate that individuals at Beza Mahafaly tend to migrate within a limited area, often only migrating to adjacent troops (Sauther and Cuozzo, unpublished data). Our data also reflect the pattern described for several modern human populations (e.g., Greene et al., 1967; Perzigian, 1975), in which an increase in tooth size corresponds to high levels of attrition and tooth wear, a condition common to the ringtailed lemurs at Beza Mahafaly (e.g., Sauther et al., 2001a, 2002; Cuozzo and Sauther, 2004a, 2004b, 2005, in press).

We recognize that these questions require additional research, and one of our long-term goals is to continue our longitudinal study of ringtailed lemur dental variation, health, and feeding ecology at Beza Mahafaly. This work will include an emphasis on individual dental life stories, in the broader context of understanding *L. catta* ecology, evolution, and life history. In addition, we plan to expand our research on temporal change and focus on the impact of human populations on the environment surrounding the Beza Mahafaly Reserve (see Whitelaw et al., 2005). As human activity has had a dramatic impact on the environment and fauna of Madagascar over the past two thousand years (e.g., Godfrey et al., 1997; Godfrey and Jungers, 2003), and has likely influenced contemporary evolution among lemurs, illustrating the effects that rapid ecological change can have on a living species has a number of direct conservation implications for Malagasy primates.

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