The Impact of Dental Impairment on Ring-Tailed Lemur Food Processing Performance

James B. Millette,[1]* Michelle L. Sauther,[1] Frank P. Cuozzo,[2] and Jenifer L. Ness[3]

[1]Department of Anthropology, University of Colorado at Boulder, 233 UCB, Boulder, CO 80309-0233
[2]Department of Anthropology, University of North Dakota, 236 Centennial Drive, Stop 8374, Grand Forks, ND 58202-8374
[3]Department of Biology, University of North Dakota, Grand Forks, ND 58202

ABSTRACT   During mastication, foods are reduced into particles suitable for swallowing and digestion. Smaller particles possess a greater surface area per unit of volume on which digestive enzymes and bacteria may work than relatively larger particles, and are thus more readily digested. As dental morphology facilitates the breakdown of diets with specific mechanical properties, extensive dental wear and/or tooth loss may impede an individual's ability to break down and exploit foods. We present data demonstrating a relationship between dental impairment and particle size in 43 fecal samples from 33 ring-tailed lemurs at the Beza Mahafaly Special Reserve (BMSR), Madagascar. All fecal samples were sifted through three sieves of decreasing size (11.2 mm, 4.75 mm, and 1.0 mm). The resulting fraction in each sieve was then weighed and assessed in relation to individual dental impairment status. With increasing wear, the percentage of each sample within the 1.0 mm sieve decreases, whereas that in the 11.2 mm sieve increases with increasing postcanine wear, although these effects are not present when limited to individuals without tooth loss. Individuals with tooth loss also demonstrate larger proportions of fecal material 1.0–4.75 mm in size. Dental impairment results in larger food particles and potentially less efficient utilization of foods. When fecal material was examined by leaf vs. fruit content, individuals with tooth loss demonstrated reduced proportions of fruit in the 1.0 mm and 11.2 mm sieves. These data suggest individuals with tooth loss consume less fruit than those without loss, potentially reflecting a reduced ability to process tamarind fruit, a key fallback resource at BMSR. Am J Phys Anthropol 148:238–248, 2012.   © 2012 Wiley Periodicals, Inc.

Teeth are the primary structures by which foods are initially processed and reduced before subsequent swallowing and digestion. For particular diets, mammalian dental morphology therefore demonstrates forms that facilitate the generation of forces necessary to cause runaway crack propagation within foods characterized by specific physical and structural properties (Lucas, 2004). For example, researchers have long noted that primarily folivorous and insectivorous species demonstrate high-cusped and crested teeth with shearing capabilities necessary to initiate and continue cracks within foods characterized by physically tough structural carbohydrates such as found within cell walls (e.g., cellulose) and chitinous insect exoskeletons. In turn, primarily frugivorous and hard object consuming taxa demonstrate morphologies of lower relief suited to breaking open the cell walls of fruits through grinding and crushing, or opening hard foods (e.g., seeds) without incurring damage to the tooth (Kay, 1975; Seligsohn, 1977; Kay et al., 1978; Yamashita, 1998; Lucas, 2004; Evans et al., 2007). Dental morphology, however, may be altered significantly through an animal's lifespan due to a variety of processes including dental disease, wear from physical interactions with food items, food processing, and masticatory behaviors (including cultural variation among humans), dental morphology and microstructure, chemical erosion, and/or physical damage resulting from exposure to high forces (Molnar, 1971, 1972; Rensberger, 1973; Graham and Burkart, 1976; Smith et al., 1977; Smith, 1984; Lanyon and Sanson, 1986; Janis and Fortelius, 1988; Teaford and Oyen, 1989; Hillson, 1996; Gandara and Truelove,

1999; Maas and Dumont, 1999; Verrett, 2001; Kaifu et al., 2003; Lucas, 2004; Lussi et al., 2004; Nussey et al., 2007). Severe wear that ablates critical functional features of the tooth, and/or tooth loss which results in the failure of occlusion between opposing positions, is presumed to hinder the breakdown and subsequent utilization of food items thus negatively impacting aspects of individual health (Gipps and Sanson, 1984), life history, reproduction (Logan and Sanson, 2002; King et al., 2005), and survival (Lucas, 2004).

A key aspect of dental function is the reduction of foods from their initial form into particles of decreased size. Breaking down food into particles permits individuals to consume food items which are too large to swallow

in their original state and/or may permit access to resources that would otherwise pass through the digestive tract unutilized [(e.g., seeds) Lucas, 2004]. Particle size may also play a role in the efficient digestion and utilization of food items as particle size corresponds to the surface area to volume ratio of ingested foods. Particles of relatively smaller size demonstrate an increased surface area to volume ratio in comparison to particles of relatively larger size, and therefore present a larger surface on which digestive enzymes and gut bacteria may act. Individuals who reduce foods into relatively smaller sized particles should thus digest and utilize foods more effectively than those who reduce foods into larger particles (McLeod and Minson, 1969; Bjorndal et al., 1990; Lentle et al., 2003; Lucas, 2004).

The impact of dental morphology on masticated food particle size distributions, and the impact of food particle size on subsequent digestion and utilization of food items, has been demonstrated for a number of mammalian species (Sheine and Kay, 1977; Kay and Sheine, 1979; Sheine, 1979; Gipps and Sanson, 1984; Lanyon and Sanson, 1986; Bjorndal et al., 1990; Lentle et al., 2003). Experiments by Bjorndal et al. (1990) demonstrate, that when digested *in vitro* in inoculant drawn from cattle rumen, grass particles of smaller size digest more completely than do particles of comparatively greater size, and also that grass particles 3 mm in size digest at a greater rate (1.7×) than 30 mm sized particles when placed in the rumen of cattle. Likewise, in their study of four wallaby species, Lentle et al. (2003) noted that reduced food particle size was associated with enhanced organic matter, neutral-detergent fiber and acid-detergent fiber digestibility. Additionally, among browser and browser/grazer wallaby species, ingested food particle sizes were of larger size than those found among grazer and grazer/browser species, suggesting that predominantly herbivorous species must more finely reduce their diets to ensure effective utilization of resources than those which persist on a less herbaceous diet (see below). Similarly, Gipps and Sanson (1984) noted that, when fed a controlled diet, ring-tailed possums (*Pseudocheirus* sp.) with significant dental wear showed reduced neutral-detergent fiber and dry matter digestion, as well as weight loss. These authors also reported that individuals with experimentally ablated dentitions had greater amounts of large food particles and vascular bundles within their stomachs but did not demonstrate weight loss, reduced digestibility, or differences in ingested food particle size, suggesting increased intake of digestible materials. Likewise, in koalas, Lanyon and Sanson (1986) noted significant tooth wear was associated with larger particle sizes in the stomach and caecum in comparison to individuals with lower wear.

Although similar datasets are limited among nonhuman primates, Sheine and Kay (1977) noted that insectivorous *Galago senegalensis* demonstrated smaller food particles in their feces than did more frugivorous *Cheirogaleus medius*. These authors suggested that the reduction of foods into finer particles by *G. senegalensis* reflects the higher proportion of insects consumed by this species and the need to break down chitinous exoskeletons into small fragments toward their efficient enzymatic digestion. This presumption is supported by later experimental work (Kay and Sheine, 1979) demonstrating that galagos more efficiently digested chitin of smaller particle sizes than they did chitin particles of larger particles. Likewise, Sheine (1979) also reported

that *Lemur catta* and *Eulemur fulvus* sbsp. digested greater amounts of dietary cellulose when presented in experimental diets in small particles (0.425–0.710 mm) than when provided in larger sized particles (0.850–1.70 mm), suggesting these species demonstrate adaptations suited toward breaking down and utilizing fibrous material, but also highlighting that particle size may play a role in the assimilation of such resources.

The extent to which particle size impacts digestion is also contingent, in part, on the nature of the diet consumed. For instance, food particle size should be of great importance for diets high in structural carbohydrates, particularly for herbaceous materials of which cellulose-based cell walls cannot be digested by mammals without microbial action within the gut (e.g., Van Soest and McQueen, 1973; Stevens, 1988; Mackie, 2002). Reducing foods into particles of small size may be of less importance than previously assumed in the digestion of herbaceous materials, provided that consumers can cause numerous cracks and fissures through the indigestible cuticle of larger sized particles. Such cracks may effectively increase the relative surface area of otherwise large sized particles (Bjorndal et al., 1990). In contrast, fruit materials may require less breakdown than do herbaceous materials as these are comparatively easy to digest. In such cases thoroughly breaking down fruits may, however, be beneficial as this permits access to resources stored within cell walls and which would otherwise be more difficult to utilize. Despite these caveats, all things being equal, individuals who maintain an ability to reduce foods into particles of smaller size will demonstrate enhanced digestive efficiency and utilization of ingested resources than those individuals who do not (e.g., Lucas, 2004).

Dental impairment in Beza Mahafaly Ring-Tailed Lemur

Lemur catta living in and around the gallery forest dominated Parcel 1 of the Beza Mahafaly Special Reserve (BMSR), Madagascar, show exceptionally high rates of tooth wear and frequencies of wear-related tooth loss, with 26.5% of individuals exhibiting the total loss (e.g., complete ablation of the crown) of at least one tooth and 6.4% of all assessed positions being absent. This is the highest reported frequency of tooth loss for any sample of extant nonhuman primates (Cuozzo and Sauther, 2006a). The loss of multiple teeth for individuals is common, with 10.8% of lemurs showing >30% loss, and 4.6% with >50% tooth loss. The highest loss observed in a living individual is 81% (Cuozzo and Sauther, 2004, 2006a).

The high frequencies of wear-related antemortem tooth loss observed among BMSR *L. catta* results primarily from the consumption of tamarind fruit (*Tamarindus indica*). Ripe tamarind fruit is a dominant dietary component during the dry season for ring-tailed lemurs living in semi-deciduous riverine gallery forest at BMSR and serves as an important fallback food resource during this period as the availability of alternative food items is limited due to seasonal effects (Sauther, 1992, 1998; Ratsirarson et al., 2001; Cuozzo and Sauther, 2004, 2006a,b; Simmen et al., 2006; Cuozzo et al., 2008; Sauther and Cuozzo, 2009). This fruit is exceptionally difficult for *L. catta* to consume as ripe tamarind is physically the largest food item eaten at BMSR, has a casing (exocarp) which is harder and tougher than any other food eaten by *L. catta*

at BMSR and also possesses tough fibers surrounding edible portions of the fruit (Cuozzo and Sauther, 2006a,b; Yamashita, 2000, 2008b; Yamashita et al., this volume). Ring-tailed lemur dental morphology appears to be poorly adapted to breaking down diets in which large, hard, and tough foods compose a major proportion of items consumed. In contrast to hard object feeding adapted species, which frequently demonstrate blunt cusp morphology and comparatively thick enamel, ring-tailed lemurs possess dental morphology characterized by elongated shearing crests and enamel which is among the thinnest observed for any extant primate taxa (e.g., Shellis et al., 1998; Godfrey et al., 2005). Ring-tailed lemur dental morphology thus appears to be adapted toward a more folivorous diet than is consumed at BMSR (Kay et al., 1978; Dumont, 1995; Yamashita, 1998; Cuozzo and Sauther, 2004, 2006a,b; Lambert et al., 2004; Godfrey et al., 2005; see also review in Cuozzo and Yamashita, 2006). Tooth wear and loss therefore appear to result from using a comparatively thin-enameled and crested tooth to process the hard and tough casing of the tamarind fruit and scraping the fruit's tough internal fibers across the tooth during consumption (Cuozzo and Sauther, 2004, 2006a,b; Cuozzo et al., 2008; Sauther and Cuozzo, 2009; Yamashita et al., this volume).

Severe tooth wear and loss is particularly common for postcanine tooth positions directly involved in tamarind fruit processing, with the first molars being the most frequently lost position, followed by (in descending order) P3, P4, and M2. Because M1 is the first permanent position to erupt, the high rate of M1 loss likely reflects an interaction between eruption schedule and tamarind consumption, which corresponds with and/or begins soon after weaning (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a). The association between loss and eruption schedule is, however, weakly linked for other tooth positions. For example, the P3 and P4 positions commonly used in tamarind fruit processing are more frequently absent than are earlier-erupting positions which are used less during tamarind fruit processing (e.g., I1, I2, and, M2). High rates of dental wear are also noted in the deciduous dentition of subadults (which demonstrate adult patterns of tamarind processing) further highlighting the role of tamarind in the generation of tooth wear and loss observed for BMSR *L. catta* and indicating that wear commences and proceeds rapidly from an early age (Cuozzo and Sauther, 2006b; Sauther and Cuozzo, 2009).

Behavior, tooth loss, and food particle size

Although dental impairment is presumed to reduce the efficiency with which foods are processed and utilized, BMSR ring-tailed lemurs have been observed to adjust their behaviors to compensate for tooth loss (Millette et al., 2009). Individuals with tooth loss show divergent food processing behaviors in comparison to those without tooth loss. For example, these individuals demonstrate longer tamarind fruit feeding bout lengths than do individuals without tooth loss, but do not show longer feeding bouts when consuming less-challenging foods which do not require extensive initial processing (e.g., small *Enterospermum pruinosum* berries which are swallowed whole without processing). These data suggest that lemurs with tooth loss may be less capable of consuming tamarind fruit than individuals without tooth loss (Millette et al., 2009). As tamarind fruit is a top fruit resource during the dry season at BMSR, the relative proportion of tamarind in the feces of individuals without tooth loss may be greater than those without loss as these lemurs may more easily access and consume greater quantities of this fruit per feeding bout.

Ring-tailed lemurs, however, may alter their behaviors to compensate for reduced tamarind fruit processing abilities. For example, individuals with tooth loss have been observed to engage in higher frequencies of licking behavior when consuming tamarind than individuals without tooth loss. Individuals have also been observed to manually process tamarind fruit and consume tamarind pods previously opened and discarded by other group members. Examination of excreted food particles may help understand the relationship of these behaviors toward the compensation for tooth loss, particularly those directed toward consumption of tamarind fruit. If these behaviors are fully compensatory, the relative proportion of fruit material within the feces of these individuals may not differ from those without tooth loss. As such, examining the relative proportion of fruit material within the feces of individuals with dental impairment in comparison to those without dental impairment may test the efficacy of these behavioral adjustments.

Study goals and hypotheses

In this article, we examine the relationship between dental impairment and (1) fecal particle size as an indicator of ingested food particle size and (2) the relative proportion of leaf matter to fruit matter with respect to fecal particle size in ring-tailed lemurs of the BMSR. We hypothesize that individuals with dental impairment will demonstrate increased fecal food particle size in comparison to those without dental impairment. We also hypothesize that individuals will demonstrate divergent patterns of processing for different types of food (e.g., fruits vs. leaves). We suggest that dentally impaired individuals will demonstrate reduced proportions of fruit material within their feces as these individuals are expected to demonstrate reduced efficiency when processing tamarind fruit.

METHODS
Study site

The BMSR (23°30′S and 44°40′E) is located in southwest Madagascar approximately 35 km northeast of the town of Betioky Sud. The reserve consists of two protected parcels, an annex connecting the two parcels and a research camp. This study was conducted using samples procured from *L. catta* living in or adjacent to Parcel 1, an 80 ha western Malagasy dry semi-deciduous gallery forest located on the western bank of the ephemeral Sakamena River (Sauther et al., 1999; Ratsirarson, 2003). Since 1979, Parcel 1 has been relatively free from anthropogenic impacts (e.g., logging or livestock grazing) by both a barbed-wire fence and an agreement by the local Mahafaly population to not graze their animals within the reserve. The eastern portion of Parcel 1 is a mature riparian deciduous and semi-deciduous forest which progressively becomes more xerophytic in western areas away from the river (Sauther, 1998; Ratsirarson, 2003). This gallery forest is dominated by tamarind (*T. indica*), particularly on the parcel's wetter eastern portion. Eastern portions of the reserve are characterized by a closed canopy of roughly 15–20 m in height and consisting primarily of tamarind, *Acacia rouvmae*,

Euphorbia tirucalli, and *Salvadora angustifolia*. Below this canopy layer, and in western portions of Parcel 1, most trees are relatively short in height ranging from 2 to 15 m. Dominant tree species in a given area of the Parcel 1 tends to follow the decreasing east–west gradient of water availability, although tamarind and *Azima tetracantha* are found throughout Parcel 1 (Sussman and Ratsirarson, 2006).

Unprotected gallery forest covering approximately 200 ha is located contiguously to the north and south borders of Parcel 1 (Sussman and Ratsirarson, 2006). These areas demonstrate reduced productivity and degradation of the forest understory due to grazing and farming (Sussman and Rakotozafy, 1994; Sauther, 1998; Sauther and Cuozzo, 2009). The quantity and quality of understory lianas and herbs available for use by ring-tailed lemurs is reduced within these areas in comparison to Parcel 1 (Sussman and Rakotozafy, 1994; Sauther, 1998; Sauther and Cuozzo, 2009). Located immediately south of Parcel 1, the camp area consists of several small administrative and research buildings, a small museum and camping facilities for researchers and visitors. These facilities include a kitchen, a closed water well, and open trash pits that are sometimes raided by several lemur groups (Sauther et al., 2006; Fish et al., 2007; Millette, personal observations). Although lemurs have been observed to procure both food and water from these sources, BMSR ring-tailed lemurs are not provisioned. Ring-tailed lemurs range through and utilize all aforementioned areas irrespective of anthropogenic alterations, with several social groups using both protected and disturbed areas (Sauther et al., 2006; Fish et al., 2007).

Dental assessment and capture protocol

Individual tooth wear and loss data were determined by F.P.C. for 33 BMSR ring-tailed lemurs during annual health assessments (see capture and assessment protocol below) conducted during the 2006, 2007 and 2008 field seasons. Tooth loss was recorded only for positions where the crown was worn to the gumline and/or was totally missing, leaving at most only worn roots (e.g., Cuozzo and Sauther, 2006a; Cuozzo et al., 2010). Such positions are not in occlusion and represent a total loss of tooth function. Of the 33 study subjects, seven individuals were found to be missing at least one tooth, with total tooth loss ranging from 8% to 56%. Of these, all but one individual demonstrated >10% tooth loss (e.g., heavy loss). When limited to the postcanine dentition, tooth loss ranged from 8% to 79%. For this study, postcanine dentition is defined as maxillary tooth positions distal to the canine, and mandibular positions distal to the lower second premolar, as this tooth is canine-like in form and function (e.g., Cuozzo and Yamashita, 2006). To provide an indicator of individual tooth wear status, a wear index was calculated. For each individual, all tooth positions were scored using a 0–5 ordinal wear scale (0 representing a low-wear state, 5 representing the total ablation of the tooth to the gumline, see Table 1 and Fig. S1). Wear indices were determined by dividing the sum of wear scores by the number of teeth present for (1) the total dental arcade and (2) for the postcanine dentition. Total wear indices ranged from 0.500 to 4.750, whereas postcanine wear ranged from 0.500 to 4.733. A complete listing of tooth wear and loss statistics for individuals used in this study is available in the Supporting Information Table S1.

All captures were conducted as part of a long-term study (since 2003) of ring-tailed lemur health, behavior,

TABLE 1. Tooth wear ordinal scale

0—unworn occlusal surface
1—small wear facets and no dentine or pulp exposure
2—large wear facets and no dentine or pulp exposure
3—some dentine and pulp exposure, few cusps still present; for canine and tooth comb, 1/2 remaining
4—pulp exposure, with cusps gone, dentine or pulp exposed across most of the surface, or partial crown remaining; for canine and toothcomb, less than 1/4 remaining
5—tooth worn to or below gum line with only roots/partial roots remaining (i.e., functional loss [see Cuozzo and Sauther, 2004, 2006a); OR no presence of the tooth remains (i.e., healed gingiva only, or in skeletal specimens remodeled alveoli)

and life history conducted by M.L.S. and F.P.C. (see Cuozzo and Sauther, 2004, 2006a,b; Sauther and Cuozzo, 2009). All lemurs were captured using a Dan-Inject blow dart system (Dan-Inject, North America, Fort Collins, CO) in conjunction with the drug Telazol® (Fort Dodge Laboratories, Fort Dodge, IA). Darting, capture, and examination protocols followed methods developed over 20 years of research and over 400 safe captures at BMSR (e.g., Sussman, 1991; Sauther et al., 2002, 2006; Cuozzo and Sauther, 2006a,b; Miller et al., 2007; Larsen et al., 2011). During each examination, a veterinarian and veterinary students were present to monitor the health of the captured lemur. All methods and materials received approval by and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committees (IACUC) of the Universities of North Dakota and Colorado-Boulder. All data collection and captures were approved by MNP (Madagascar National Parks, formerly ANGAP), the body governing research in Madagascar's protected areas.

Fecal methods

Forty-three fecal samples were collected during the dry seasons (June–August) of 2006, 2007, and 2008 from 33 study subjects. Ten fecal samples were collected from individuals demonstrating tooth loss, whereas 33 samples were collected from individuals without tooth loss. Fecal samples were collected from excreta produced during annual health inspections, either while lemurs were being examined and assessed, or from the portable kennels in which the lemurs recover, following their release. Following collection, samples were washed with water through three sieves of decreasing size (11.2 mm, 4.75 mm, and 1.0 mm), producing three sub-samples of the following sizes: 1.0–4.75 mm, 4.75–11.2 mm, and >11.2 mm. Seeds were not removed from the sample, with most of these deposited in the 4.75 mm and 11.2 mm sieves (see Fig. 1). Samples were then dried and transported to the University of Colorado at Boulder where the mass of each fraction was weighed. As samples collected during field observations were often impossible to collect in their entirety, and some of each sample <1 mm in size was lost during sieving, each sieved proportion was assessed in relation to the total dry mass recovered following sieving. Each resulting mass proportion was then assessed in relation to individual wear and loss status using non-parametric methods (e.g., Mann–Whitney U and Spearman *rho*). Non-parametric methods were utilized as masticated food particle sizes are typically not normally distributed (see Lucas, 2004). For each test, statistical significance was set at the $\alpha = 0.05$ level.

Fig. 1. Food particle size fractions were produced by sieving each fecal sample through sieves of decreasing size (A). Each fraction was then dried individually before being weighed and assessed as a proportion of the total mass of recovered material (B). Image (C) demonstrates fecal materials trapped within the 11.2 mm sieve, including tamarind seeds and leaf material.

TABLE 2. Mean percentage of total fecal mass for each sieved fraction in relation to tooth loss status

Sieve size fraction	1.0–4.75 mm		4.75–11.2 mm		>11.2 mm	
	% total mass	*sd*	% total mass	*sd*	% total mass	*sd*
Tooth loss (*N* = 10)	22.4	7.5	47.9	12.3	29.7	12.6
No tooth loss (*N* = 33)	36.6	16.3	42.0	11.7	21.3	15.2
Mann–Whitney *U* score	75.0		114.0		110.0	
P value	*0.0097*		0.1426		0.1127	
>10% tooth loss (*N* = 9)	21.5	7.3	48.6	12.2	29.9	13.3
<10% tooth loss (*N* = 34)	36.5	16.1	42.0	12.1	21.5	15.0
Mann–Whitney *U* score	62.0		111.0		104.0	
P value	*0.0066*		0.6217		0.1422	
Postcanine loss (*N* = 10)	22.4	7.5	47.9	12.3	29.7	12.6
No postcanine loss (*N* = 33)	36.6	16.3	42.0	11.7	21.3	15.2
Mann–Whitney *U* score	75.0		114.0		110.0	
P value	*0.0097*		0.1426		0.1127	

$p < 0.05$

To assess the potential relationship between tooth loss and the consumption of divergent food item types, for a 20-fecal sub-sample (10 from individuals with tooth loss and 10 from those without loss), the relative proportion of fruit to leaf mass was determined within each size fraction. For each sieve, fruit material and leaf material were manually separated. These proportions were then weighed and assessed in relation to their total mass. The relative proportions of these materials within each sieve size were then assessed in relation to tooth loss status using non-parametric methods (e.g., Mann–Whitney *U*). Statistical significance was set at α = 0.05 level. Although leaf material (e.g., undigested leaf portions, leaf vasculature, and stems) was easily distinguished from fruit material (e.g., seeds, tamarind shell, and remnants of fruit "meat"), it was not possible to reliably distinguish the species of each leaf, although several fruit species were readily identifiable (e.g., *E. pruinosum* and *T. indicia*). As species could not be reliably determined

for leaves, a simple leaf/fruit distinction was utilized to assess the relationship between dental impairment and the relative proportion of dietary components within each sieved portion. Insect material was not observed, and thus not considered, when assessing fecal contents.

RESULTS

Dental impairment and particle size

Tooth loss status was associated with fecal particle size. Individuals with tooth loss demonstrated relatively smaller proportions of material 1.0–4.75 mm in size than did individuals without tooth loss. This pattern also holds true for individuals with greater than 10% tooth loss, and also when assessed with respect to the postcanine dentition. Unexpectedly, no differences were found between individuals with tooth loss and without tooth loss for material recovered in the 4.75–11.2 mm or >11.2

mm fractions. This pattern remains when examined in terms of the postcanine dentition and/or limited to individuals with greater than 10% tooth loss (Table 2 and Fig. 2). When particle sizes were examined with respect to tooth wear indices, increasing wear was associated with a smaller proportion of particles in the small 1.0–4.75 mm proportion. When limited to postcanine wear, significantly more particles were also present in the large >11.2 mm sample with increasing wear scores. When examined with respect to tooth wear indices, patterns observed with respect to tooth loss status hold remarkably well. This is not unexpected as individuals with extensive tooth loss demonstrate significantly higher rates of tooth wear, as wear is the primary cause of tooth loss in this population (e.g., Cuozzo and Sauther, 2006a). However, when assessed by excluding individuals without tooth loss, but demonstrating tooth wear, no significant patterns for any of the three size categories were present (Table 3 and Fig. 3).

Tooth loss is associated with greater proportions of leaves and reduced proportions of fruit within the 1.0–4.75 mm sample and the >11.2 mm sample. A similar but non-significant pattern is also present in the 4.75–11.2 mm sample. These data indicate that leaves are present in greater quantities in the feces of individuals with tooth loss and suggest that these individuals ingest fewer fruits than do individuals without tooth loss during BMSR's dry season (Fig. 4 and Table 4).
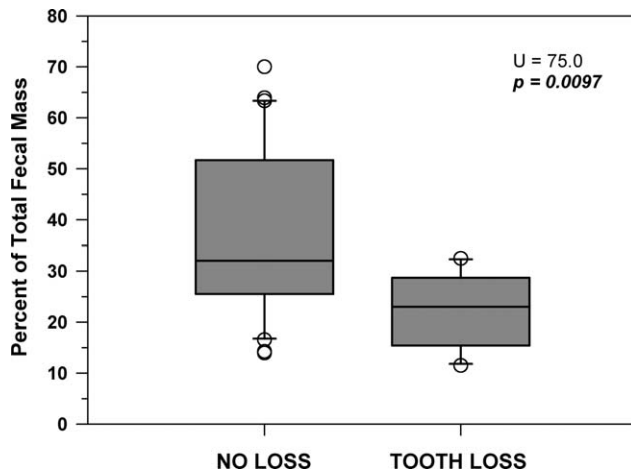
DISCUSSION
Dental impairment and food processing

Our data indicate a link between dental impairment and fecal food particle size. Individuals with tooth loss demonstrate significantly higher proportions of material in the 1.0–4.75 mm sample. Wear index was also associated with fecal particle size for the 1.0–4.75 mm sample and also the >11.2 mm sample when examined in terms of postcanine wear. Therefore, fecal particle size provides a means for assessing the impact of dental impairment on an individual's ability to process and utilize food items among ring-tailed lemurs. Individuals with significant dental impairment, such as severe tooth wear and/or tooth loss, demonstrate a reduced ability to break down foods into particles of small size in comparison with those with lower amounts of dental impairment. Given the link between food particle size and the effective utilization of food items, these lemurs may demonstrate a comparatively lower capacity to digest and harness nutrients of foods consumed. This may be especially true in terms of capacity to utilize leaves, which appear to be a major dietary component for lemurs with tooth loss in this study and given that food particle size-related loss of cellulose digestion has been reported for *L. catta* by Sheine (1979).

No differences were found between individuals with and without tooth loss for the 4.75–11.2 mm or >11.2 mm categories. One explanation for these data is that the generation of particles in these size ranges is attainable regardless of tooth loss status, although further breakdown is not readily possible for dentally impaired individuals. A second explanation is that dentally impaired indi-
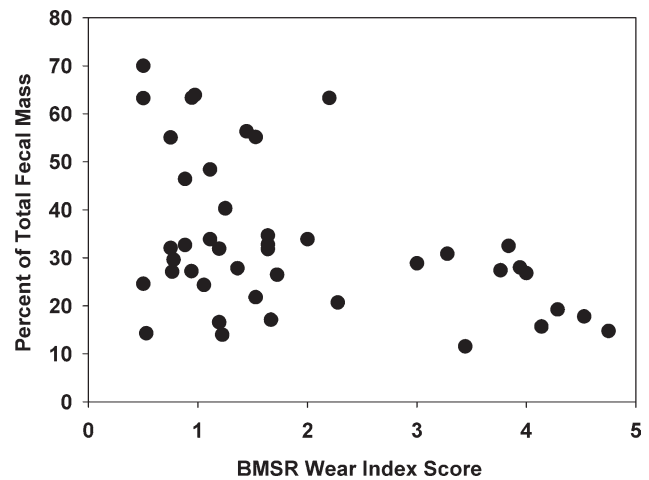

Fig. 2. Percentage of total fecal mass accounted for by the 1.0–4.75 mm sieve fraction based on tooth loss status. Individuals without tooth loss demonstrate significantly greater proportion of their fecal materials within this sample than do individuals with tooth loss. No differences were noted for either the 4.75–11.2 mm or >11.2 mm fractions between individuals with and without tooth loss.

Fig. 3. The relationship between tooth wear status and fecal food particle size for the 1.0–4.75 mm sized sample. Increasing tooth wear status is associated with a reduced proportion of fecal material within the 1.0–4.75 mm sized fraction.

TABLE 3. *Relationship between tooth wear status and sieved fecal food particle size*

| | | Sieved Fraction Size | | | | | |
| | | 1.0–4.75 mm | | 4.75–11.2 mm | | >11.2 mm | |
Tooth wear status	N	rho	P	rho	P	rho	P
Total wear	43	−0.379	*0.014*	0.257	0.095	0.282	0.067
Postcanine wear	43	−0.387	*0.012*	0.244	0.114	0.307	*0.047*
Total wear (no loss)	33	−0.145	0.411	0.182	0.303	0.151	0.393
Postcanine wear (no loss)	33	−0.174	0.326	0.169	0.339	0.187	0.289

$p < 0.05$

viduals may be selecting items which more easily fragment than do those without impairment. We suggest, however, that individuals with tooth loss or extensive wear do not divergently select food items as *L. catta* feed predominantly in a synchronous manner where all members of a social group consume a single species or type of food simultaneously (Sauther et al., 1999) and tend to focus on a narrow variety and limited number of food species as they become seasonally available (Sauther, 1998). Patterns of food consumption should thus be similar between individuals irrespective of tooth loss status. Additionally, if impaired individuals are selecting foods based on ease of breakdown, their observed particle size distributions should be similar to those without impairment. As this is not the case, it appears that dentally impaired individuals comparatively are less capable of reducing food items into particles of small size.

Individuals with tooth loss demonstrate relatively higher proportions of leaves and reduced proportions of fruit in their fecal matter. One explanation for these findings is that individuals may be selectively consuming leaves in lieu of fruit. Alternatively, these data may reflect an inability to access fruit resources, particularly

Fig. 4. Percentage of leaf material within each fecal sieve size for individuals with and without tooth loss. Individuals with tooth loss demonstrated increased proportions of leaf material within their fecal material than did individuals without tooth loss for both the 1.0–4.75 mm and >11.2 mm fractions than did individuals without tooth loss. These data suggest that individuals with tooth loss ingest relatively lower proportions of fruit material than do individuals without tooth loss.

tamarind fruit, which is a primary dry-season fallback food that is exceptionally challenging to process (e.g., Sauther and Cuozzo, 2009). Dentally impaired individuals may not be able to access tamarind as efficiently as those without dental impairment, thus reducing the relative percentage of fruit within each fecal sample. This interpretation is supported by observations that individuals with tooth loss demonstrate difficulty opening tamarind pods and exhibit longer feeding bout lengths for tamarind fruit (Millette et al., 2009, personal observations). Given that herbaceous material is of comparatively lower quality than the ripe tamarind fruit consumed during the dry season, which is a high quality food rich in sugar (see Yamashita, 2008a), and observations that dentally impaired individuals do not as finely comminute leaf material (see Fig. 1C), it is likely that they show reduced energetic intake in comparison to individuals without dental impairment.

When limited to individuals without tooth loss, tooth wear indices are not related to food particle size. These data suggest that tooth wear alone does not result in reduced masticatory abilities for ring-tailed lemurs at BMSR and may provide support for the hypothesis that teeth have evolved in a manner where functionality is maintained despite the presence of wear. As primate teeth do not regenerate or remodel their unworn morphology, they should evolve in a manner which permits the efficient breakdown of diets consisting of food items of specific physical and structural properties through wear (Rensberger, 1973; Kay, 1981; Teaford, 1983; Lanyon and Sanson, 1986; Ungar and M'Kirera, 2003; Dennis et al., 2004). For example, among folivorous species, differential wear between enamel and dentin may result in the maintenance of dental function through the exposure of shearing crests where dentin ablates at a higher rate than does enamel (Rensberger, 1973; Lanyon and Sanson, 1986; King et al., 2005).

Several researchers have demonstrated that functional aspects of primate dental morphology are maintained through the course of wear. For example, using three-dimensional Geographical Information Systems-based topographic methods on worn teeth of chimpanzees and gorillas, Ungar and M'Kirera (2003; see also M'Kirera and Ungar, 2003) found that despite reductions in overall slope and relief with wear, these species remain constant in their topographic angularity, a measure of the average change in slope of the tooth associated with the breakdown of tough material. In this case, gorillas maintained comparatively higher angularity through the course of wear than did chimpanzees, consistent with their (in comparison to chimpanzees) tougher and more folivorous diet. As such, these authors suggest that angularity represents a means through which dental function
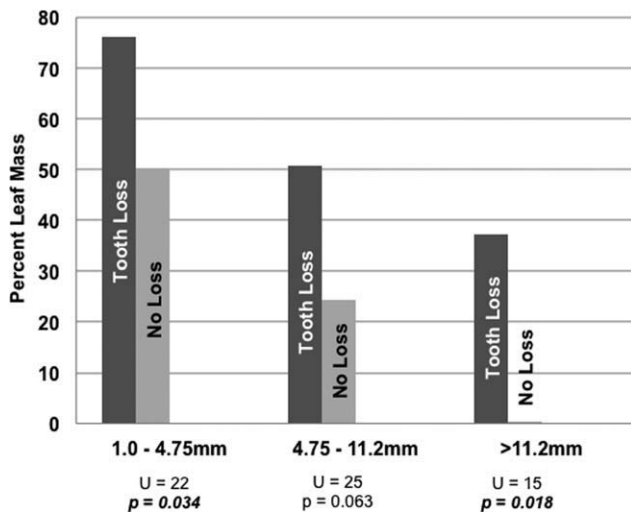
TABLE 4. *Type of food within each sieved fraction by tooth loss status*

Sieve fraction size	Loss status	N	% fruit	sd	% leaf	sd
1.0–4.75 mm	Tooth loss	10	23.9	24.6	76.1	24.6
	No tooth loss	10	49.7	29.1	50.3	29.1
	U-Score = 22	*P = 0.034*				
4.75–11.2 mm	Tooth loss	10	49.3	28.8	50.7	28.8
	No tooth loss	10	75.7	28.4	24.3	28.4
	U-Score = 25	*P = 0.063*				
>11.2 mm	Tooth loss	10	62.8	39	37.2	39
	No tooth loss	8[a]	99.6	0.7	0.4	0.7
	U-Score = 15	*P = 0.018*				

[a] No > 11.2 mm sized particles were present for two individuals without tooth loss.
$p < 0.05$

is maintained despite the onset of wear. Similar maintenance of angularity until extreme wear has been reported for howling monkeys by Dennis et al. (2004). Likewise, King et al. (2005) found that extreme dental wear was associated with increased maternal infant mortality among *Propithecus edwardsi* during periods of low rainfall, although individuals with lower wear did not demonstrate rainfall-linked patterns of reduced infant survival.

Ring-tailed lemurs at BMSR may demonstrate a similar maintenance of dental function through the course of wear as, when limited to individuals without tooth loss, increasing wear status is not associated with the reduction of foods into larger sized particles. As a result, wear alone appears insufficient to limit an individual's ability to efficiently masticate foods into particles. The finding that wear status is associated with increasing proportions of larger sized food particles when individuals with tooth loss are included is not unexpected, as loss represents the total elimination of function for a given tooth position. Nevertheless, the hypothesis that dental function is maintained despite wear for BMSR *L. catta* remains speculatory. Individuals without tooth loss may simply not possess wear of sufficient severity to impact particle size. Individuals with extensive wear also likely show comparatively higher levels of wear than do individuals without tooth loss. These data do, however, provide initial evidence that dental function is maintained despite wear among BMSR lemurs prior to the onset of tooth loss.

Behavior and dental impairment

Although food particle size appears related to dental impairment in BMSR ring-tailed lemurs, the impact of dental impairment on these individuals is not yet fully understood. As we have discussed elsewhere (Millette et al., 2009), ring-tailed lemurs compensate for tooth loss through behavioral mechanisms related to food processing. Individuals with tooth loss may gain access to foods by simply spending more time for processing each individual food item. Also, individuals have been observed processing foods using alternative means, including nondental food processing such as licking food items and/or use of the hands. Alternatively, individuals with dental impairment utilize foods that have been previously processed and discarded by others (Cuozzo and Sauther, 2006a). Individuals with tooth loss, particularly extensive tooth loss, have also been observed to remain active during periods of group inactivity and resting during the early afternoon, using this period instead to feed, forage, and groom (Millette et al., 2009).

Individuals may also compensate for dental impairment using strategies that have not yet been investigated. For example, dentally impaired individuals may preferentially select food items which are less challenging to process and consume. Such alterations to the diet may explain differences in the contents of fecal samples assessed during this study. If this is the case, fecal particle size may also be impacted by food choice. Although the presence and direction of any such change remains speculatory, dental impairment is still expected to result in the consumption of larger sized food particles for a given diet.

Our data indicate that dental impairment is associated with increased food particle sizes and reduced fruit intake. Behaviors associated with compensation for tooth loss do not appear to enhance the efficiency with which food items are broken down into particles, or to confer compensatory food processing abilities. Behavioral responses to tooth loss thus appear to reflect compensation through increasing overall food intake and/or access to foods, but likely do not impact the utilization of food resources once acquired, processed, and ingested.

CONCLUSIONS

Our data indicate that individuals with dental impairment demonstrate divergent patterns of fecal food particle size than do individuals without dental impairment. Tooth loss and wear appear to negatively impact an individual's ability to breakdown of food items and indicate that dental impairment leads to reduced masticatory performance. The presence of larger food particle sizes within the feces of individuals with dental impairment indicates that these individuals likely utilize ingested food items less effectively. The extent to which the increased particle size impacts ring-tailed lemur health, survival, and reproduction is not yet known or well understood. Ring-tailed lemurs with extensive tooth loss living at BMSR, however, have been observed to survive for extended periods (e.g., survival for >5 years in a near-edentulous state) while in good health and do not demonstrate reduced reproductive success in comparison to those without tooth loss (Cuozzo and Sauther, 2004, 2006a,b; Cuozzo et al., 2010). The impact of tooth loss alone, and thus increased particle size, is not inextricably linked to individual health and survival in this population. We suggest that individuals with tooth loss attempt to compensate for this reduction of masticatory abilities through behavioral mechanisms, including alterations to activity budget and food processing behaviors (see Millette et al., 2009). These alterations, however, do not appear to result in similar particle size distributions between individuals with and without dental impairment. These data indicate that behaviors used in compensation for dental impairment do not act through reducing food particle size. Rather, such behaviors likely increase overall access to foods and/or permit the initial breakdown foods, which could otherwise not be consumed.

Data presented here also suggest that individuals with tooth loss demonstrate divergent patterns of food consumption, ingesting more leaves than they do fruit material. We suggest that this is potentially a function of reduced tamarind fruit processing capabilities among individuals with tooth loss, as this fruit is exceptionally difficult for *L. catta* to process and consume. Alternatively, these individuals may be emphasizing leaves over fruit, regardless of a reduced ability to comminute leaves into finely sized particles and a presumably impaired capacity to extract nutrients from this resource. Although we as of yet have no feeding behavior data regarding patterns of leaf consumption among individuals with dental impairment, these individuals may be attempting to offset reductions in their ability to utilize this resource by increasing the total volume of leaves consumed. Such alterations to feeding behavior may be particularly prevalent if access to important alternative foods is restricted by dental impairment, as is likely the case with ripe tamarind fruit. Our ongoing work at BMSR will further clarify such aspects of food item choice and consumption in relation to dental impairment.

Tooth wear was not associated with increased particle sizes when individuals with tooth loss were excluded. These data indicate that tooth loss is a key element in

the reduction of masticatory efficiency for individuals living at BMSR, and that dental function may be maintained through the course of wear prior to tooth loss. This interpretation supports the hypothesis that masticatory function is maintained among individuals with tooth wear and is only reduced when extensive wear and/or tooth loss is present.

In conclusion, our data suggest the following is true for ring-tailed lemurs at BMSR:

1. Tooth loss is associated with reduced proportions of small sized particles 1.0–4.75 mm in size but is not associated with divergent patterns for particles 4.75–11.2 mm or >11.2 mm in size. As a result, individuals with tooth loss may less effectively process food items and may utilize foods less efficiently than do those without tooth loss.
2. Increasing dental wear is associated with fewer proportions of 1.0–4.75 mm sized particles and, when limited to postcanine wear scores, also greater proportions of large >11.2 mm sized particles. No such differences are present when individuals with tooth loss are removed from the sample. Tooth wear alone may thus not result in a loss of dental function among BMSR *L. catta*.
3. Individuals with tooth loss demonstrate greater proportions of leaf material in their fecal material than do individuals without tooth loss, suggesting that individuals with tooth loss consume less fruit during the dry season at BMSR.

ACKNOWLEDGMENTS

LITERATURE CITED

Bjorndal KA, Bolton AB, Moore JE. 1990. Digestive fermentation in herbivores: effect of food particle size. Physiol Zool 63:710–721.

Cuozzo FP, Sauther ML. 2004. Tooth loss, survival and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids. J Hum Evol 46:623–631.

Cuozzo FP, Sauther ML. 2006a. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. J Hum Evol 51:490–505.

Cuozzo FP, Sauther ML. 2006b. Temporal change in tooth size among ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar: effects of an environmental fluctuation. In: Jolly A, Sussman RW, Koyama, N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p 343–366.

Cuozzo FP, Sauther ML, Gould L, Sussman RW, Villers L, Lent C. 2010. Variation in dental wear and tooth loss among known-aged older ring-tailed lemurs (*Lemur catta*): a comparison between wild and captive individuals. Am J Primatol 71:1026–1037.

Cuozzo FP, Sauther ML, Yamashita N, Lawler RR, Brockman DK, Godfrey LR, Gould L, Jacky Youssouf IA, Lent C, Ratsirarson J, Richard AF, Scott JR, Sussman RW, Villers LM, Weber MA, Willis G. 2008. A comparison of salivary pH in sympatric wild lemurs (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. Am J Primatol 70:363–371.

Cuozzo FP, Yamashita N. 2006. Impact of ecology of the teeth of extant lemurs: a review of dental adaptations, function, and life history. In: Gould L, Sauther ML, editors. Lemurs: ecology and adaptation. New York: Springer. p 67–96.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125:152–161.

Dumont ER. 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. J Mammal 76:1127–1136.

Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

Fish KD, Sauther ML, Loudon JE, Cuozzo FP. 2007. Coprophagy by wild ring-tailed lemurs (*Lemur catta*) in human-disturbed locations adjacent to the Beza Mahafaly Special Reserve, Madagascar. Am J Primatol 69:713–718.

Gandara BK, Truelove EL. 1999. Diagnosis and management of dental erosion. J Contemp Dent Pract 1:1–17.

Gipps JM, Sanson GD. 1984. Mastication and digestion in *Pseudocheirus*. In: Smith AP, Hume ID, editors. Possums and gliders. Sydney: Australian Mammal Society. p237–246.

Godfrey LR, Semprebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuozzo FP, King SJ. 2005. New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825–854.

Graham EE, Burkart J. 1976. A preliminary analysis of antemortem tooth loss among the Fremont. Am Antiq 41:534–537.

Hillson S. 1996. Dental anthropology. Cambridge: Cambridge University Press.

Janis CM, Fortelius M. 1988. On the means where by mammals achieve increased functional durability of their dentitions with special reference to limiting factors. Biol Rev 63:197–230.

Kaifu Y, Kasai K, Townsend GC, Richards LC. 2003. Tooth wear and the "design" of the human dentition: a perspective from evolutionary medicine. Yearb Phys Anthropol 46:47–61.

Kay RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195–216.

Kay RF. 1981. The nut crackers: a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141–151.

Kay RF, Sheine WS. 1979. On the relationship between chitin particle size and digestibility in the primate *Galago senagalensis*. Am J Phys Anthropol 50:301–308.

Kay RF, Sussman RW, Tattersall I. 1978. Dietary and dental variations in the genus *Lemur*, with comments concerning dietary-dental correlations among Malagasy primates. Am J Phys Anthropol 49:119–128.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, God-frey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci USA 102:16579–16583.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am J Phys Anthropol 125:363–368.

Lanyon JM, Sanson GD. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. II. implications of tooth wear in nutrition. J Zool 209:169–181.

Larsen RS, Moresco A, Sauther ML, Cuozzo FP. 2011. Field an-esthesia of wild ring-tailed lemurs (*Lemur catta*) using Tilet-amine-Zolazepam. Medetomidine, and Butorphanol. J Zoo Wild Med 42:75–87.

Lentle RG, Hume ID, Stafford KJ, Kennedy M., Springett BP, Haslett SJ. 2003. Observations on fresh forage intake, ingesta particle size and nutrient digestibility in four species of mac-ropod. Aust J Zool 51:627–636.

Logan M, Sanson GD. 2002. The association of tooth wear with sociality of free-ranging male koalas (*Phascolarctos cinereus* Goldfuss). Aust J Zool 50:621–626.

Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press.

Lussi A, Jaeggi T, Zero D. 2004. The role of diet in the aetiology of dental erosion. Caries Res 38:34–44.

M'Kirera F, Ungar PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. Am J Primatol 60:31–41.

Maas MC, Dumont ER. 1999. Built to last: the structure, func-tion and evolution of primate dental enamel. Evol Anthropol 8:133–152.

Mackie RI. 2002. Mutualistic fermentative digestion in the gas-trointestinal tract: diversity and evolution. Integr Comp Biol 42:319–326.

McLeod MN, Minson DJ. 1969. Sources of variation in the in vitro digestion of tropical grasses. J Brit Grass Soc 24:244–249.

Miller DS, Sauther ML, Hunter-Ishikawa M, Fish KD, Cul-bertson H, Cuozzo FP, Campbell TW, Chavey S, Nachreiner R, Rumbeiha W, Stacewicz-Sapantzakis M, Lappin MR. 2007. Biomedical evaluation of free-ranging ring-tailed lemurs (*Lemur catta*) in three habitats at the Beza Maha-faly Special Reserve, Madagascar. J Zoo Wildl Med 38:201–216.

Millette JB, Sauther ML, Cuozzo FP. 2009. Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. Am J Phys Anthropol 140:120–134.

Molnar S. 1971. Human tooth wear, tooth function, and cultural variability. Am J Phys Anthropol 46:447–454.

Molnar S. 1972. Tooth wear and culture: a survey of tooth func-tions among some prehistoric populations. Curr Anthropol 13:511–526.

Nussey DH, Metherell B, Moyes K, Donald A, Guinness FE, Clutton-Brock TH. 2007. The relationship between tooth wear, habitat quality and late-life reproduction in a wild red deer population. J Anim Zool 76:402–412.

Ratsirarson J. 2003. Reserve Speciale de Beza Mahafaly. In: Goodman SM, Benstead JP, editors. The natural history of Madagascar. Chicago: The University of Chicago Press. p1520–1525.

Ratsirarson J, Randrianarisoa J, Ellis E, Emady J, Efitroarany, Ranaivonasy J, Razanajaonarivalona EG, Richard AF. 2001. Serie Sciences Biologiques: No 18 - Beza Mahafaly: Ecologie et Realites Socio-economiques. Antananarivo: Recherches Pour Le Developpement.

Rensberger JM. 1973. An occlusion model for mastication and dental wear in herbivorous mammals. J Paleontol 47:515–528.

Sauther ML. 1992. Effect of reproductive state, social rank and group size on resource use among free-ranging ring-tailed lemurs (*Lemur catta*) of Madagascar. Unpublished Ph.D. Dis-sertation. Department of Anthropology, Washington University.

Sauther ML. 1998. The interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur con-servation. Folia Primatol Suppl 69:309–320.

Sauther ML, Cuozzo FP. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitats. Am J Phys Anthropol 140:671–686.

Sauther ML, Fish KD, Cuozzo FP, Miller DS, Hunter-Ishikawa M, Culbertson H. 2006. Patterns of health, disease and behav-ior among wild ring-tailed lemur, *Lemur catta*: effects of habi-tat and sex. In: Jolly A, Sussman RW, Koyama N, Rasamima-nana H, editors. Ringtailed lemur biology. New York: Springer. p 313–331.

Sauther ML, Sussman RW, Cuozzo FP. 2002. Dental and gen-eral health in a population of wild ring-tailed lemurs: a life history approach. Am J Phys Anthropol 117:122–132.

Sauther ML, Sussman RW, Gould L. 1999. The socioecology of the ring-tailed lemur: thirty-five years of research. Evol Anthropol 8:120–132.

Seligsohn D. 1977. Analysis of species-specific molar adaptations in strepsirrhine primates. Contrib Primatol 11:1–116.

Sheine WS. 1979. The effect of variations in molar morphology on masticatory effectiveness and digestion of cellulose in pro-simian primates. Ph.D. Dissertation. Department of Anthro-pology, Duke University.

Sheine WS, Kay RF. 1977. An analysis of chewed food particle size and its relationship to molar structure in the primates *Cheirogaleus medius* and *Galago senagalensis* and the insecti-voran *Tupaia glis*. Am J Phys Anthropol 47:15–20.

Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:597–522.

Simmen B, Sauther ML, Soma T, Rasamimanana HR, Sussman RW, Jolly A, Tarnaud L, Hladik A. 2006. Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamima-nana H, editors. Ringtailed lemur biology. New York: Springer. p55–68.

Smith BH. 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. Am J Phys Anthropol 63:39–56.

Smith JD, Genoways HH, Jones JK. 1977. Cranial and dental anomalies in three species of platyrrhine monkeys from Nicar-agua. Folia Primatol 28:1–42.

Stevens CE. 1988. Comparative physiology of the vertebrate di-gestive system. New York: Cambridge University Press.

Sussman RW. 1991. Demography and social organization of free-ranging Lemur catta in the Beza Mahafaly Reserve, Madagascar. Am J Phys Anthropol 84:43–58.

Sussman RW, Rakotozafy A. 1994. Plant diversity and struc-tural analysis of a tropical dry forest in southwestern Mada-gascar. Biotropica 26:241–254.

Sussman RW, Ratsirarson J. 2006. Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p43–51.

Teaford MF. 1983. Differences in molar wear gradient between adult macaques and langurs. Int J Primatol 4:427–444.

Teaford MF, Oyen OJ. 1989. Differences in the rate of molar wear between monkeys raised on different diets. J Dent Res 68:1513–1518.

Ungar PS, M'Kirera F. 2003. A solution to the worn tooth co-nundrum in primate functional anatomy. Proc Nat Acad Sci USA 100:3874–3877.

Van Soest PJ, McQueen RW. 1973. The chemistry and estima-tion of fibre. Proc Nutr Soc 32:123–130.

Verrett RG. 2001. Analyzing the etiology of an extremely worn dentition. J Prosthodont 10:224–233.

Yamashita N. 1998. Functional dental correlates of food proper-ties in five Malagasy lemur species. Am J Phys Anthropol 106:169–188.

Yamashita N. 2000. Mechanical thresholds as a criterion for food selection in two prosimian primate species. In: Spatz HC, Speck T, editors. Proceedings of the 3rd plant biomechanics

conference, Freiburg-Badenweiler August 27th to September 2nd. Stuttgart: Thieme Verlag. p 590–595.

Yamashita N. 2008a. Chemical properties of the diets of two lemur species in southwestern Madagascar. Int J Primatol 29:339–364.

Yamashita N. 2008b. Food physical properties and their relationship to morphology: the curious case of kily. In: Vinyard C, Ravosa MJ, Wall CE, editors. Primate craniofacial function and biology. New York: Kluwer Academic Press. p 387–406.

Yamashita N, Cuozzo FP, Sauther ML. Interpreting food processing through dietary mechanical properties: a *Lemur catta* case study. Am J Phys Anthropol, in press.