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Behavioral Responses to Tooth Loss in Wild Ring-Tailed Lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar

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ABSTRACT Severe dental wear and tooth loss is often assumed to impede the processing, breakdown, and energetic conversion of food items, thereby negatively impacting individual health, reproduction, and survival. Ring-tailed lemurs at the Beza Mahafaly Special Reserve demonstrate exceptionally high frequencies of severe dental wear and antemortem tooth loss, yet often survive multiple years with these impairments. To test the hypothesis that these lemurs mitigate tooth loss through behavioral adjustments, we collected 191 h of observational data from 16 focal subjects, eight without tooth loss and eight with between 3% and 44% loss. These data indicate dentally-impaired ring-tailed lemurs show compensatory behaviors consistent with the demands of living in a social group. During early afternoon (12:00–14:30 h) individuals with loss showed trends towards higher frequencies of foraging and grooming, while individuals without loss rested significantly more often. Individuals with >10% loss (n = 7) showed higher frequencies of feeding, foraging, and grooming, and lower frequencies of resting during this period than individuals with <10% loss (n = 9). Individuals with tooth loss maintained relatively higher levels of feeding and foraging throughout the day. These individuals licked tamarind fruit at higher frequencies, likely spending more time softening it before ingestion. These individuals did not demonstrate longer feeding bouts overall, although bouts involving tamarinds were significantly longer. Individuals with marked toothcomb wear engaged in higher rates of certain types of allogrooming, demonstrating that social behaviors are used to compensate for reduced grooming efficiency. These data have implications for interpreting behavioral responses to dental impairment in the fossil record. Am J Phys Anthropol 140:120–134, 2009. ©2009 Wiley-Liss, Inc.

Among primates and other mammals, dental morphology corresponds to the processing, mechanical breakdown, and ingestion of food items with specific mechanical and structural properties (Kay, 1975; Seligsohn, 1977; Kay et al., 1978; Yamashita, 1998; Lucas, 2004; Evans et al., 2007; see review in Cuozzo and Yamashita, 2006). Severe tooth wear and/or tooth loss may therefore impede the breakdown and subsequent energetic conversion of key foods, negatively impacting aspects of an individual's health, life history, reproduction, and survival (Gipps and Sanson, 1984; Lanyon and Sanson, 1986; Logan and Sanson, 2002a,b; King et al., 2005).

A long-term, comprehensive study of general and dental health of ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve (BMSR), Madagascar illustrates a pattern of rapid tooth loss, and exceptionally high frequencies of severe wear and antemortem tooth loss (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a,b). In a study of 83 living lemurs at BMSR, 26.5% exhibited extensive tooth wear resulting in the complete loss (e.g., total ablation of the crown) of at least one tooth (Cuozzo and Sauther, 2006a). For all tooth positions assessed within this population (n = 2,988), 6.4% were scored as absent, the highest frequency of tooth loss among any reported sample of extant nonhuman primates (See Tables 3a,b in Cuozzo and Sauther, 2006a). Extensive tooth loss is also common, with 10.8% of individuals demonstrating greater than 30% loss, and 4.6% showing greater than 50% tooth loss. The greatest amount of loss in a living individual is 81% (Orange 170, [Cuozzo and Sauther, 2004, 2006a]). Figure 1 illustrates the extensive tooth loss in a living BMSR ring-tailed lemur in comparison to an individual with limited wear.

Sources and patterns of tooth loss for ring-tailed lemurs at BMSR

In contrast to most primate populations in which tooth loss is a function of dental disease and/or damage (see discussion in Cuozzo and Sauther, 2006a), tooth loss among the BMSR ring-tailed lemurs is primarily the result of severe and extensive wear (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a,b). Mammalian dental wear reflects a complex interaction of potential variables. This includes: behavior (including culture among humans), a food item's mechanical properties, food availability and quality, food processing and mastication, dental morphology, and enamel microstructure (Molnar,

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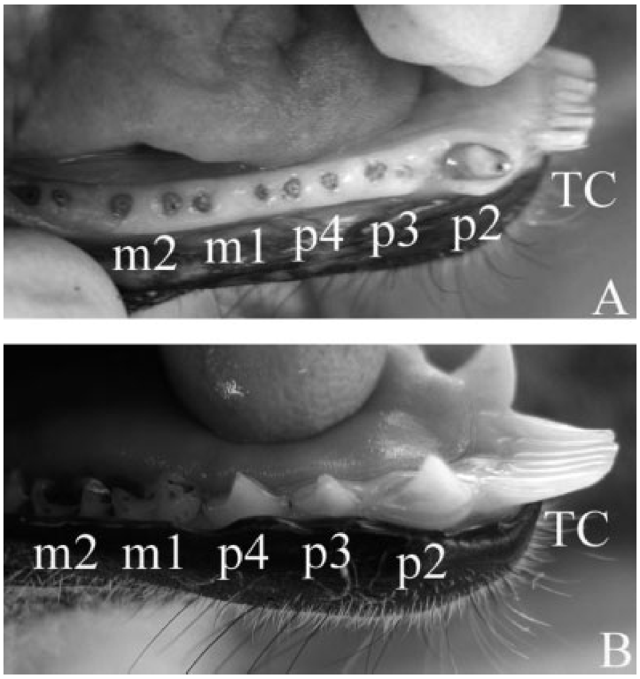

Fig. 1. Tooth loss in a living ring-tailed lemur. (**a**) Absence of *Lemur catta* mandibular teeth, with only worn roots remaining (Yellow 195). Also note the worn toothcomb (TC). (**b**) Normal (limited wear) mandibular teeth in *Lemur catta* (Teal 205). Note the unworn toothcomb (TC) (Reproduced from Cuozzo and Sauther. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. Journal of Human Evolution 51:490–505. © 2006 with permission Elsevier.).

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). Among ring-tailed lemurs living in the gallery forests at BMSR, tooth wear and subsequent loss are primarily caused by the consumption of ripe tamarind fruit (*Tamarindus indica*) (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a,b; Cuozzo et al., 2008). Ripe tamarind fruit is the hardest and toughest of all foods consumed by ring-tailed lemurs at BMSR in terms of its mechanical properties (Yamashita, 1996, 2000, 2008), and is a key fallback food during the resource-depleted dry season for ring-tailed lemurs inhabiting the riverine gallery forests at BMSR (Sauther, 1992, 1998; Cuozzo and Sauther, 2006b, in press; Simmen et al., 2006; Sauther and Cuozzo, in press). Tamarind fruit is also the largest fruit consumed at BMSR by ring-tailed lemurs, processing of which requires contact with a large portion of the toothrow (Cuozzo and Sauther, 2006a,b).

Mechanical properties play a central role in how food items fragment during processing and subsequent mastication. Hard foods prevent the initial propagation of cracks during processing, and require high initial forces to commence mechanical failure of the food item. In turn, tough food items demonstrate significant plasticity before failure, and resist the propagation of cracks once crack formation has been initiated, thereby arresting further breakdown (Strait, 1997; Lucas, 2004; Cuozzo and Yamashita, 2006). As tamarind fruit demonstrates both hard and tough properties (Yamashita, 2000, 2008), this is an exceptionally challenging resource to process, breakdown, and consume. Also, tannins in tamarind fruit, which may reduce the lubricating properties of saliva thus increasing friction between teeth (Prinz and Lucas, 2000; but see de Wijk and Prinz, 2005), likely contribute to the pattern of wear in the BMSR lemurs (Cuozzo et al., 2008). Although consumption of hard and/or tough foods is frequently associated with thick dental enamel and blunt cusp morphology, *Lemur catta* possess among the thinnest molar enamel known among extant primates, and relatively (in comparison to other lemurids) elongated shearing crests similar to folivorous lemurs, for example *Propithecus*. (Kay et al., 1978; Dumont, 1995; Yamashita, 1998; Cuozzo and Sauther, 2004, 2006a,b; Lambert et al., 2004; Lucas, 2004; Godfrey et al., 2005). Consequently, ring-tailed lemur dental morphology appears ill-suited to processing large hard and tough tamarind fruit. In contrast, sympatric *Propithecus,* despite also frequently consuming tamarind fruit, rarely display severe molar wear and exhibit little tooth loss (Cuozzo and Sauther, 2006a, in prep.). Such patterns among *Propithecus* are primarily related to their focus on unripe tamarind fruit, which is neither as hard nor as tough as the ripe tamarind fruit typically consumed by ring-tailed lemurs (Cuozzo and Sauther, 2006a; Yamashita, 2003, 2008).

Thus, patterns of tooth wear and loss observed among ring-tailed lemurs at BMSR may reflect a potential "ecological mismatch" or evolutionary disequilibrium between this species' dental morphology and the physical properties of a diet reliant upon ripe tamarind fruit (Cuozzo and Sauther, 2006a, in press; Cuozzo et al., 2008; Sauther and Cuozzo, in press). As we argue elsewhere, this "disequilibrium" appears the result of an over-reliance on this fruit in the tamarind dominated gallery forests of southern Madagascar (Cuozzo and Sauther, in press, in prep; Sauther and Cuozzo, in press). Although *Tamarindus indica* appears native to Madagascar (Du Puy et al., 2002), there is no evidence for the temporal depth of *Lemur catta* dependence on this fruit where it appears. Also, in the spiny forests of southern Madagascar, where tamarind is rare (e.g., Tsimanampesotse National Park), ring-tailed lemurs display limited tooth wear and rare tooth loss (Cuozzo and Sauther, in prep; Sauther and Cuozzo, in press), further suggesting disequilibrium.

Tamarind pods are a large and challenging food to process. Tamarinds have a hard outer shell, and portions must be bitten off prior to ingestion; this is normally done using the postcanine teeth (Fig. 2, [Sauther, 1992]). As a result, severe wear and tooth loss occurs most frequently in the postcanine positions (see Table 1) and is most common for positions involved directly in tamarind fruit processing (Cuozzo and Sauther, 2006a). As such, M1 is the most frequently lost tooth position, followed (in descending order) by 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 coincides 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, P3 and P4 positions are more frequently absent than earlier-erupting positions (e.g. I1, I2, and M2). These data suggest that the frequency of absence for a given position is related primarily to tooth function, and highlights the key role of tamarinds in the generation of tooth wear and antemortem loss in ring-tailed lemurs (Cuozzo and Sauther, 2006a).

Fig. 2. A ring-tailed lemur processing a tamarind fruit, a primary source of tooth wear at BMSR. (Reproduced from Cuozzo and Sauther. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. Journal of Human Evolution 51:490–505. © 2006 with permission Elsevier.) (Photo: M.L.S.).

Impacts of tooth loss on ring-tailed lemur survival and health

Severe wear and tooth loss, such as that observed among ring-tailed lemurs at BMSR, is often assumed to prohibit individual access to key food items, ultimately resulting in death (Lucas, 2004). Although tooth wear and loss likely impedes the processing, breakdown, and consumption of tamarinds and other key food items, at least three individuals have been observed to live in a nearly-edentulous state for up to three years (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a). Individuals with tooth loss have also been observed to survive into old age while remaining reproductively active. Although part of our ongoing long-term project, preliminary data on reproduction and infant survival for these individuals suggests that tooth loss greater than 10% (see description below) does not predict lack of infant survival through weaning. Specifically, all three female individuals included in this study with greater than 10% tooth loss (from 14% to 44%) demonstrate infant survival through weaning (Cuozzo and Sauther, in prep). This pattern is in contrast to that described for *Propithecus* at Ranomafana National Park, where degree of tooth loss was associated with infant survival during periods of reduced rainfall (King et al., 2005). Tooth loss is furthermore only loosely associated with observed patterns of overall health. In a survey of general health in 69 individuals, only three of nine animals rated in "fair" or "poor" health showed >10% tooth loss. Likewise, three individuals with >50% tooth loss were observed to be in "good" or "fair" health (Cuozzo and Sauther, 2004).

Behavioral responses to tooth loss

One way ring-tailed lemurs at BMSR may compensate for tooth loss is through behavioral mechanisms. Primates have been shown to modify their behaviors to deal with a variety of energetic challenges. For a number of primates, it has been demonstrated that lactating females must alter their activity budgets to accommodate the energetic costs of nursing (see review in Dufour

TABLE 1. Individual tooth loss and impairment status

Individual ID	Sex	Loss status	% Tooth loss Overall	% Tooth loss Anterior	% Tooth loss Posterior	Notes on dental pathologies present
Blue 138	F	Loss	44	0	100	Remaining teeth heavy wear and few occlusal surfaces, toothcomb worn
Black 226	M	Loss	22	13	87	Moderate to heavy wear throughout dental arcade
Black 6	M	Loss	19	0	100	Moderate to heavy wear throughout, toothcomb damage
Orange 249	M	Loss	19	0	100	Moderate to heavy wear throughout dental arcade, toothcomb damage
Green 459 (TF)	F	Loss	17	0	100	Heavy wear throughout dental arcade, some molar decay, broken I1
Orange 156	F	Loss	14	40	60	Moderate to heavy wear throughout dental arcade
Green 209	M	Loss	14	40	60	Moderate to heavy wear throughout dental arcade, some molar decay
Green 34 (TF)	F	Loss	3	0	100	Some molar decay, broken upper LM3
Lt. blue 130	M	No loss	0	0	0	Minor toothcomb wear
Orange 168	F	No loss	0	0	0	No tooth loss or impairment
Blue 227	F	No loss	0	0	0	No tooth loss or impairment
Orange 231	F	No loss	0	0	0	No tooth loss or impairment
Blue 250	M	No loss	0	0	0	No tooth loss or impairment
Lt. blue 253	M	No loss	0	0	0	Severe malocclusion, heavy wear on upper left canine
Blue 259	M	No loss	0	0	0	No tooth loss or impairment
Orange 300	F	No loss	0	0	0	No tooth loss or impairment

and Sauther, 2002). For example, lactating gelada baboons increase energy intake by beginning to feed earlier in the day and withdrawing from less important social relationships (Dunbar, 1983). Likewise, lactating yellow baboon females increase time spent feeding in exchange for time normally spent resting or socializing (Altmann, 1980). However, to our knowledge no researchers have yet investigated behavioral responses to dental impairment among wild nonhuman primates, although several such studies have been conducted on nonprimate mammals (Gipps and Sanson, 1984; Perez-Barberia and Gordon, 1998; Logan and Sanson, 2002a,b,c). Among male koalas (*Phascolarctos cinereus*), Logan and Sanson (2002a,b,c) found that individuals compensated for extensive tooth wear by increasing time engaged in feeding behaviors while reducing behaviors not directly related to somatic maintenance. In comparison to individuals with low to medium wear, those with severe dental wear increased time spent feeding by 62%, while simultaneously increasing the volume of food consumed by 41% and chews per leaf consumed by 116% (Logan and Sanson, 2002c). In turn, time spent walking (e.g., traveling) or engaged in movement was significantly reduced in individuals with advanced tooth wear, as was home range size (Logan and Sanson, 2002b). Individuals with heavy wear also engaged in fewer social behaviors, suggesting a general reduction of non-maintenance expenses in favor of compensatory feeding (Logan and Sanson, 2002a). Increases in food volume intake similar to those observed in *P. cinereus* have also been reported for ring-tailed possums (*Pseudocheirus*) with experimentally ablated dentition (Gipps and Sanson, 1984). In addition, among captive red deer (*Cervus elaphus*), individuals with reduced masticatory efficiency (as measured by molar occlusal surface area) were reported to spend more time chewing food items than those with relatively higher masticatory efficiency (Perez-Barberia and Gordon, 1998).

Ring-tailed lemurs with tooth loss at BMSR may alter their activity budget in a manner consistent with that observed among *P. cinereus* by increasing time spent feeding and foraging while reducing resting and other non-maintenance behaviors. Individuals may also compensate by spending more time processing food items. In contrast to koalas that are primarily solitary (Mitchell, 1990), ring-tailed lemurs live within cohesive multimale/multifemale social groups (e.g., Sauther et al., 1999). Dentally-impaired individuals are thus expected to be limited in terms of behaviors that may compensate for tooth loss, as they must also follow the overall patterns of behavior within their social group. Impaired individuals may therefore increase maintenance behaviors primarily during periods of relative group inactivity, which among ring-tailed lemurs occurs during a synchronous resting period during the early afternoon (Sauther, 1992). Such alterations to behavior are plausible given that resting provides a reservoir of unused time that may be accessed when necessary for the completion of a required activity (Dunbar, 1988). Feeding and foraging in response to dental impairment is therefore expected to be associated with reduced resting, particularly during periods when others are inactive. Likewise, as reductions in resting are associated with reduced social activity among nonhuman primates (Dunbar, 1988), dentally-impaired individuals may also decrease social interactions during this period to forage for and consume food items. In addition, ring-tailed lemurs groom orally using the lower incisors and canines of the toothcomb (Buettner-Janusch and Andrew, 1962; Sauther et al., 2002; Swindler, 2002). Individuals with tooth loss demonstrate higher frequencies of ectoparasites (e.g., mites) than do those without tooth loss, suggesting this impairment impacts grooming efficiency (Sauther and Cuozzo, unpublished data). Individuals with tooth loss may therefore engage in comparatively higher frequencies of grooming to compensate for reduced grooming efficiency.

Initial observations conducted at BMSR suggest ring-tailed lemurs may compensate for tooth loss through adjustments in food processing behaviors (Cuozzo and Sauther, 2006a). Observed patterns of dental wear and feeding behavior indicate that ring-tailed lemurs process most hard food items with their postcanine teeth (Sauther et al., 2002; Yamashita, 2003). Individuals with postcanine wear may process food items with challenging physical properties (e.g., tamarind fruit) on anterior regions of the toothrow, as suggested by the presence of worn maxillary canines in individuals with severe postcanine wear and loss (Cuozzo and Sauther, 2006b). Field observations (Cuozzo and Sauther, 2006a) suggest that dentally-impaired individuals may compensate by consuming food items previously processed and discarded by other group members. Individuals with tooth loss may also process and consume food items through use of nondental means. Ring-tailed lemurs commonly lick larger food items with the tongue during feeding bouts, particularly during consumption of tamarind fruit (Sauther, 1992; Millette, personal observation). Such behavior may facilitate the physical breakdown of foods through use of the tongue instead of the teeth, and may furthermore deposit saliva, thereby softening the food items prior to dental breakdown. Licking behavior may thus be utilized more frequently by individuals demonstrating tooth loss.

Study aims and hypotheses

In this study, we characterized and quantified behaviors associated with tooth loss among ring-tailed lemurs at BMSR. We examined two primary mechanisms by which individuals may compensate for tooth loss: 1) alterations to activity budget, and 2) food processing behaviors. Because of its status as a major fallback resource (Cuozzo and Sauther, 2006a,b, in press; Sauther and Cuozzo, in press), and its challenging mechanical properties, special emphasis was placed upon behaviors used to process tamarind fruit. We tested the following hypotheses, expecting individuals with tooth loss to:

1. Spend a greater portion of their total activity budget engaged in maintenance behaviors involving the teeth (feeding, foraging, and grooming) and less time engaged in resting or movement than do individuals without tooth loss, particularly during periods of the day when individuals without tooth loss are inactive.
2. Process food items on the anterior toothrow more frequently than do individuals without tooth loss.
3. Engage in higher frequencies of licking to process and consume food items than do individuals without tooth loss.
4. Spend more time processing food items than do individuals without tooth loss, as indicated by feeding bouts of longer average length.

METHODS

Study site

The Beza Mahafaly Special Reserve (BMSR) (23°30′ S, 44°40′ E) consists of two forest parcels largely protected from human impact for over 20 years, a recently annexed addition connecting the two parcels, and a research camp. This study was conducted in areas within and adjacent to Parcel 1, an 80 ha gallery forest located along the western bank of the Sakamena River (Sauther et al., 1999; Ratsirarson, 2003). The eastern portion of Parcel 1 is a mature riparian deciduous and semideciduous forest that becomes more xerophytic as one moves west away from the river (Sauther, 1998; Ratsirarson, 2003). Areas immediately outside Parcel 1 demonstrate anthropogenically-reduced productivity and degradation of the forest understory resulting from the grazing and farming practices of local Mahafaly agro-pastoralists (Sauther et al., 2006). Within these areas the availability of understory lianas and herbs is reduced in comparison to Parcel 1 (Sussman and Rakotozafy, 1994; Sauther, 1998). Located immediately adjacent to Parcel 1, the camp consists of several small buildings used for administrative and research purposes and camping facilities for researchers and visitors. The camp also features an outdoor kitchen with associated open trash pits that are sometimes raided by several lemur groups (Fish et al., 2007). Although these human-derived resources are utilized by some lemurs, there is no intentional provisioning of this population. Ring-tailed lemurs utilize all aforementioned areas irrespective of anthropogenic alterations, with some groups using both reserve and anthropogenically-disturbed areas (Sauther et al., 2006).

BMSR is characterized by a highly seasonal pattern of rainfall with distinct dry (April-November) and wet seasons (December-March). Rainfall averages 550 mm per year with greater than 50% of precipitation (>100 mm per month) falling from December to February. In contrast, rainfall from June to October averages less than 10 mm per month (Sauther, 1998; Ratsirarson et al., 2001). Resource availability corresponds to patterns of rainfall with peak food availability occurring during the month of February and lowest food availability during July (Yamashita, 1996; Sauther, 1998). The behavioral data we present were collected during the period of least food availability, from June 2 to August 5, 2006, when tamarind is most often relied upon (Sauther, 1998; Gemmill and Gould, 2008; Sauther and Cuozzo, in press).

Study sample

The population of ring-tailed lemurs at BMSR has been studied extensively for more than 20 years. As a result of this research, individuals living inside and near Parcel 1 are easily identified by a collar/numerical identification system (Sauther et al., 1999; Gould et al., 2003; Sussman and Ratsirarson, 2007; Gemmill and Gould, 2008). Behavioral observations were conducted on 16 collared focal individuals (8 male and 8 female) selected based on the presence or absence of tooth loss and/or dental impairment as assessed during the 2003–2006 field seasons (Cuozzo and Sauther 2004, 2006a; see below for assessment procedure). Based upon presence or absence of tooth loss during the 2004–2005 field seasons, 13 initial focal individuals (8 females, 5 males) were placed *a priori* into "loss" and "no loss" samples. Individuals with "loss" demonstrate complete ablation of at least one tooth crown worn to or below the gumline (following Cuozzo and Sauther, 2004, 2006a). Two additional individuals without tooth loss (Light Blue 253 and Light Blue 130) and one individual with tooth loss (Orange 249) were added following the start of observations based upon assessments conducted during the 2006 field season. Dental evaluations were conducted during the 2006 field season for all focal individuals, with the exception of one individual (Green 209), who was last examined during the 2005 field season. Tooth loss within the sample ranged from 3% to 44%. Loss and impairment status for each focal animal are reported in Table 1. Focal animals were drawn from six social groups inhabiting areas: 1) entirely within Parcel 1 (Green and "Trois Fromage," three individuals), 2) exclusively outside of Parcel 1 (Black and Light Blue, four individuals), and 3) both within and outside of Parcel 1 (Orange and Blue, nine individuals).

Capture protocol and dental evaluations

Ring-tailed lemurs at BMSR were captured using a Dan-Inject blow dart system (Dan-Inject, North America, Fort Collins, CO) and the drug Telazol® (Fort Dodge Laboratories, Fort Dodge, IA). Doses were determined based on protocols developed over 20 years and over 400 safe captures of ring-tailed lemurs at BMSR (e.g., Sussman, 1991; Sauther et al., 2002, 2006; Cuozzo and Sauther, 2006a,b; Miller et al., 2007). All darting was conducted by a Malagasy field assistant with over 20 years of darting experience. All captures occurred as early as possible in the morning to allow each lemur adequate time to recover. A trained veterinarian and veterinary students were onsite to monitor the health of each individual lemur. After tooth loss, dental impairment, biometric, and overall health data were collected (see protocol below), lemurs were placed in covered mesh cages and/or dog kennels, and kept in a quiet place for recovery. Upon recovery, individuals were released in the area where they were originally captured (normally within 6 h). Following standards outlined by the U.S. CITES Management Authority (a unit of the U.S. Fish and Wildlife Service), all team members used protective surgical masks and gloves to preclude disease transfer while handling lemurs. 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: 1) the University of North Dakota, and 2) the University of Colorado. Data collection in Madagascar was conducted with approval of ANGAP (Association Nationale pour la Gestion des Aires Protégées), the body governing research in Madagascar's protected areas.

Dental evaluations were conducted by F.P.C. while animals were sedated and immobilized. For each tooth position, tooth loss was recorded only if no trace of the tooth was present (e.g., no root remnants), or if the tooth crown was completely worn to or below the gumline with only the roots remaining (see Fig. 1a). If any remnant of the crown was present, teeth were not scored as absent. In addition to tooth loss, tooth wear was assessed for each position using a 0–5 ordinal scale (Table 2). As part of an ongoing research program on dental health, ecology, behavior, and life history within this population, a complete set of dental impressions was collected for each individual using custom-built impression trays and

TABLE 2. Gross 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)

President Plus Jet Regular Body polyvinylsiloxane impression material (Coltene-Whaledent, Mawah, NJ).

Behavioral methods

J.B.M. collected 191 h of quantitative behavioral data from June 2 to August 5, 2006. All observations were conducted during the dry season, at the period of lowest resource availability (Sauther, 1992, 1998; Simmen et al., 2006; Gemmill and Gould, 2008). General activity budget data were collected using 3-min interval instantaneous focal animal sampling (see Altmann, 1974; Martin and Bateson, 2007) across a 90 min focal follow. For each instantaneous point observation, the following data were recorded: focal animal ID, observation time, behavioral state, behavior direction, social partner ID, nearest neighbor ID, nearest neighbor distance, substrate use, location, and notes collected *ad libitum*. As ring-tailed lemurs engage in both nonsocial grooming (autogrooming) and social grooming (allogrooming) behaviors, grooming form and directionality were recorded. Grooming directionality was classified using the following categories: 1) "self-directed" autogrooming, 2) allogrooming "directed" from the focal individual towards a social partner, 3) allogrooming "received" from a social partner, 4) "mutual" bidirectional allogrooming, in which a focal animal directs grooming towards a social partner while simultaneously receiving grooming from that social partner, and 5) "directionality unknown." Food item type and species were recorded for all feeding events. All instantaneous behaviors and food types were recorded using an ethogram developed for use with ring-tailed lemurs at BMSR (see Sauther, 1992). Food species was determined using a database of known foods (see Sauther, 1992) or through identification of food item samples by members of the BMSR ecological monitoring team trained in local botany.

To further assess tooth loss-related differences in feeding and food processing behaviors, a second data set specific to feeding was recorded simultaneously to that collecting general activity budget data. As such, all observed occurrences of feeding were recorded and timed to the nearest second. To differentiate feeding from foraging (searching for, but not ingesting food items), feeding is defined as all behavior associated with the physical ingestion of food items and includes the initial processing, physical breakdown (e.g., chewing), and swallowing of food items. Feeding bouts started at the time of initial food processing and ended once the focal animal stopped ingesting or chewing food items for period of 15 s, or transitioned to a new food species. Bout end time was recorded as the last second an animal was seen to ingest or chew food. Feeding was not recorded if an animal processed a food item but did not subsequently ingest the item. For each feeding event, the following were recorded: focal animal ID, bout start and end time, food item type, and food item species, location on the toothrow used in processing and use of the tongue to lick food items. Processing of foods upon the incisors or canines was defined as "anterior" processing, while use of the cheek teeth was defined as "postcanine" processing. When food items were processed in more than one location during a single feeding bout, processing location was defined as the area of the toothrow most frequently used during that bout. Licking was recorded if the tongue was used to process at least one food item during a feeding bout. During bouts in which observation conditions precluded accurate assessments for licking behavior or position of food item processing, "Unknown" was recorded.

Sampling strategy

Focal animals were sampled nonrandomly to continuously maintain an approximately equal number of follows between individuals. To control for variation in activity related to the time of day, each individual was followed for a similar amount of time during four time-periods: early morning (7:55–9:29), late morning (9:30–11:59), early afternoon (12:00–14:29), and late afternoon (14:30–15:45). Follows were terminated if the focal individual remained out-of-sight for three consecutive observations. Follows with three or more out-of-sight observations (>10% of observations per follow) were excluded from analysis. Individuals were observed a maximum of two follows per day, although at least one full time period separated repeat observations.

Data and statistical methods

All observations were recorded electronically using Microsoft Pocket Excel (Microsoft Corporation, Redmond, WA) with a Hewlett-Packard IPAQ Personal Digital Assistant (Model 2200, Hewlett-Packard Company, Palo Alto, CA). Initial data processing and statistical analyses were conducted using Microsoft Excel (Microsoft Office Excel 2003, Microsoft Corporation, Redmond, WA). Significant differences in activity budgets for resting, movement, and maintenance behaviors (grooming, feeding and foraging) were assessed for each behavior using the student's t-test. To determine time of day-related differences in these behaviors, student's t-tests were also conducted for each of the four time-of-day intervals. Feeding bout lengths for food item types were assessed using student's t-tests. Because of the directional nature of the study hypotheses, all t-tests conducted were one-tailed. All t-tests were conducted using SPSS statistical software (SPSS version 10.0, SPSS Inc. Chicago, IL). Chi-square or Fisher's exact tests were used to evaluate between sample differences in initial food processing location and frequency of licking behavior. Chi-square and Fisher's exact tests were conducted using an online contingency table calculator available through the web-

TABLE 3. Total daily behavior by tooth loss status

Behavior	Loss (N = 8) % Time	Loss SD	No loss (N = 8) % Time	No loss SD	*df*	*t*-Value	Sig. (P =)
Feed	23	5	21	6	14	−0.791	0.221
Forage	5	23	4	3	14	−0.782	0.224
Groom	9	4	7	3	14	−0.804	0.217
Movement	6	2	7	3	14	0.354	0.364
Rest	53	11	57	10	14	0.917	0.187

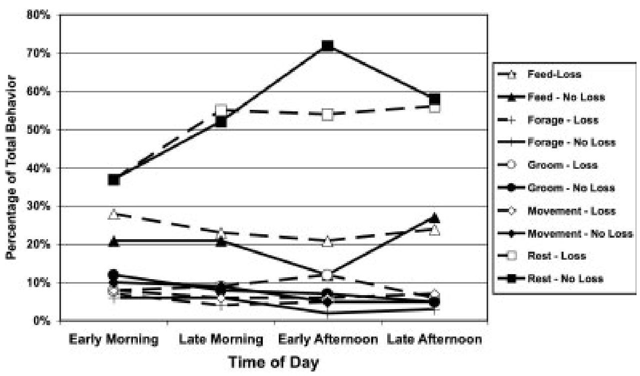

Fig. 3. Variation in total behavior by time of day and tooth loss status.

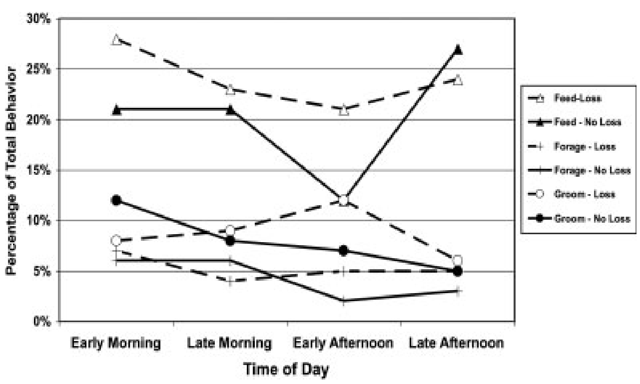

Fig. 4. Variation in maintenance behaviors by time of day and tooth loss status.

site of St. Johns University, Department of Physics (http://www.physics.csbsju.edu/stats/contingency_NROW_NCOLUMN_form.html). For all tests, significance was set at the $\alpha = 0.05$ level ($P < 0.05$).

RESULTS

Activity budget

No significant differences were present between the "loss" and "no loss" samples in total resting behavior, movement, or maintenance behaviors (Table 3). During early afternoon, individuals with tooth loss demonstrated significantly lower frequencies of resting (P = 0.044) than did individuals without tooth loss. Trends towards higher frequencies of foraging (P = 0.063) and total grooming (P = 0.086) for individuals with tooth loss were also present during the early afternoon (Figs. 3 and 4, Table 4). No significant differences were found between samples during the early morning, late morning, or late afternoon for resting, movement, feeding, foraging, or grooming (Figs. 3 and 4, Table 4). The lack of significance for behaviors across the total activity budget and for grooming, foraging, and feeding during the early afternoon may reflect disparities in the severity of tooth loss between focal subjects. Individuals with low levels of tooth loss (<10% total loss: three or fewer teeth missing; ring-tailed lemurs normally possess 36 teeth) may demonstrate fewer compensatory behaviors in comparison to those with more extensive tooth loss (>10%). When focal animals were recategorized into categories of "no/low loss" (0–10% loss) and "heavy loss" (>10% tooth loss), shifting Green (Trois Fromage) 34 who was missing only one tooth as of 2006 to the "no/low loss" group, no significant differences are present for total resting behavior, movement, or maintenance behaviors, although trends (P = 0.083) towards higher rates of grooming and reduced resting behavior (P = 0.08) are present (Table 5). However, significant differences are present between "no/low loss" and "heavy loss" samples during the early afternoon when "heavy loss" individuals demonstrate higher rates of feeding (P = 0.038), foraging (P = 0.037), and grooming (P = 0.025) and reduced rates of resting

TABLE 4. Total behavior by tooth loss status and time of day

Behavior	Loss (N = 8) % Time	Loss SD	No loss (N = 8) % Time	No loss SD	*df*	*t*-value	Sig. (P =)
Early morning							
Feed	28	15	21	14	14	−0.867	0.200
Forage	7	5	6	7	14	−0.275	0.394
Groom	8	5	12	16	14	0.701	0.247
Move	8	9	10	10	14	0.487	0.317
Rest	37	12	37	9	14	0.173	0.432
Late morning							
Feed	23	6	21	9	14	−0.577	0.287
Forage	4	2	6	2	14	1.197	0.126
Groom	9	7	8	5	14	−0.483	0.318
Move	6	3	9	6	14	1.153	0.134
Rest	55	12	52	12	14	−0.399	0.348
Early afternoon							
Feed	21	16	12	11	14	0.385	0.113
Forage	5	3	2	3	14	0.557	0.063
Groom	12	9	7	3	8.48[a]	−1.492	0.086
Move	6	5	5	6	14	−0.156	0.439
Rest	54	23	72	16	14	1.832	0.044
Late afternoon							
Feed	24	12	27	12	14	0.643	0.265
Forage	5	4	3	3	14	−1.109	0.143
Groom	6	2	5	4	14	−0.245	0.404
Move	7	3	5	3	14	−0.878	0.197
Rest	56	19	58	12	14	0.238	0.407

[a] Equal variances not assumed, corrected t-test used.

TABLE 5. Total daily behavior by heavy loss and no/low loss status

Behavior	Heavy loss (N = 7) % Time	Heavy loss SD	No/low loss (N = 9) % Time	No/low loss SD	df	*t*-Value	Sig. (P =)
Feed	24	5	21	6	14	0.969	0.175
Forage	5	2	4	2	14	0.645	0.265
Groom	9	4	7	2	14	1.463	0.083
Movement	7	2	7	3	14	0.160	0.438
Rest	51	10	58	9	14	−1.484	0.080

TABLE 6. Total behavior by heavy loss and no/low loss status and time of day

	Heavy loss ($N = 7$)		No/low loss ($N = 9$)				
Behavior	% Time	SD	% Time	SD	*df*	*t*-Value	Sig. ($P =$)
Early morning							
Feed	27	17	22	13	14	0.696	0.249
Forage	7	5	6	6	14	0.345	0.368
Groom	8	6	12	15	14	−0.774	0.226
Move	6	8	11	10	14	−0.969	0.175
Rest	38	12	37	9	14	0.192	0.425
Late morning							
Feed	22	6	21	9	14	0.287	0.389
Forage	4	3	6	2	14	−1.348	0.100
Groom	10	7	7	5	14	0.985	0.171
Move	7	3	8	6	14	−0.729	0.239
Rest	54	12	53	12	14	0.132	0.449
Early afternoon							
Feed	23	15	11	11	14	1.913	0.038
Forage	5	4	2	2	14	1.935	0.037
Groom	13	9	6	3	14	2.156	0.025
Move	7	5	5	6	14	0.661	0.505
Rest	49	19	74	16	14	−2.891	0.006
Late afternoon							
Feed	24	13	27	11	14	−0.414	0.343
Forage	5	4	4	3	14	0.778	0.225
Groom	6	2	5	4	14	0.317	0.738
Move	8	3	5	3	14	1.479	0.081
Rest	55	20	59	13	14	−0.489	0.316

($P = 0.006$). In addition, "heavy loss" individuals demonstrate a trend towards higher rates of movement ($P = 0.081$) during the late afternoon (Table 6).

As noted earlier, there was a trend towards higher frequencies of total grooming for individuals with tooth loss and significantly higher frequencies of total grooming for individuals with >10% loss during the early afternoon. Because *L. catta* grooms specifically with the toothcomb it might be expected that toothcomb loss and or toothcomb wear would affect rates of grooming. When grooming behavior is assessed by toothcomb wear status, individuals demonstrating moderate to severe toothcomb wear (wear categories 2–5) engage in significantly higher rates of overall mutual allogrooming ($P = 0.036$) than those without toothcomb wear or those demonstrating only small wear facets resulting from occlusion (wear categories 0–1). These individuals also demonstrate a trend towards higher rates of autogrooming ($P = 0.059$) and total grooming [($P = 0.074$) Table 7]. As expected, during the early afternoon these individuals also engaged in higher rates of total grooming ($P = 0.040$) and mutual allogrooming ($P = 0.045$) than did those without toothcomb wear, although rates of autogrooming did not differ significantly during this period ($P = 0.093$). Individuals with toothcomb wear also demonstrated a trend ($P = 0.052$) towards higher rates of mutual allogrooming during the late afternoon. Against expectations, individuals without toothcomb wear showed a trend ($P = 0.089$) towards higher rates of received allogrooming during the early morning (Table 8).

Food processing

No significant differences were found with respect to the location on the toothrow (anterior vs. posterior) used to process food items between "loss" and "no loss" individuals (Table 9). Tamarind accounts for 74% ($N = 233/316$) of all food items processed posteriorly. Individuals with tooth loss did not process tamarinds on the anterior toothrow at a higher frequency than did those without loss (Table 10). Tamarind fruit accounted for the majority (87%, $N = 201/231$) of observed licking bouts. Individuals with tooth loss demonstrated significantly higher frequencies ($P = 0.002$) of licking than did individuals without tooth loss (Table 11). When limited to tamarind, differences for licking behavior remained significant ($P < 0.001$, see Table 12).

TABLE 7. Grooming form as a percent of total behavior by toothcomb status

	Wear ($N = 8$)		No wear ($N = 8$)				
Grooming form	% Time	SD	% Time	SD	*df*	*t*-Value	Sig. ($P =$)
Autogroom	6.53	2.97	4.59	1.44	14	1.664	0.059
Receive	0.36	0.47	0.46	0.40	14	−0.452	0.329
Direct	0.79	0.96	0.95	1.21	14	−0.284	0.391
Mutual	1.38	1.07	0.56	0.28	7.93[a]	2.072	0.036
Total	9.06	3.79	6.67	2.29	14	1.629	0.074

[a] Equal variances not assumed, corrected *t*-test used.

Feeding bout length

No significant differences were present in the average bout length for leaves. A trend ($t = -1.66$, $P = 0.06$) towards longer fruit feeding bouts was present for individuals with tooth loss (Table 13, Fig. 5). When delineated between individuals with no/low loss and heavy loss, significant differences ($t = 2.001$, $P = 0.033$) were present in time spent consuming fruit. Individuals with extensive tooth loss also demonstrate a trend ($t = 1.578$, $P = 0.069$) towards longer feeding bouts across all food items (Table 14). At 27% of the total diet, tamarind fruit appears to be the source of this variation, with individuals exhibiting tooth loss demonstrating significantly ($P < 0.001$) longer feeding bouts for tamarinds. Bout length for the most common food item fed on during this study, mantsaka fruit (*Enterospermum pruinosum*, 30% of total diet), does not differ significantly between individuals with tooth loss and those without tooth loss (Table 15, Fig. 6).

DISCUSSION

Behavioral responses to tooth loss

Overall, the presence of tooth loss was not associated with significantly higher frequencies for feeding, foraging, grooming, or reduced total frequencies for resting or movement. Significant differences in resting behavior were present between groups during the early afternoon. Although individuals without tooth loss increase resting behavior, those with tooth loss remain active during this period. Although between-group frequencies of feeding are not statistically significant, the "loss" sample demonstrates a trend ($P = 0.063$) towards higher rates of foraging. Foraging while other social group members rest likely permits individuals to locate and consume foods while simultaneously reducing competition for food items. This hypothesis is supported by *ad libitum* observations of two older female individuals with extensive tooth loss (Orange 156, 14% loss; Blue 138, 44% loss) who regularly moved away from their social groups during the early afternoon. Orange 156 was also observed to

TABLE 8. Grooming form as a percent of total behavior by time of day in relation to toothcomb wear

Form	Wear (N = 8) % Time	Wear (N = 8) SD	No wear (N = 8) % Time	No wear (N = 8) SD	*df*	*t*-Value	Sig. (P =)
Early morning							
Autogroom	7.98	5.23	6.45	7.21	14	0.484	0.318
Receive	0	0.00	0.97	1.83	7[a]	−1.499	0.089
Direct	0	0.00	2.70	6.40	7[a]	−1.201	0.135
Mutual	0.66	1.86	1.71	2.46	14	−0.962	0.177
Total	8.63	5.89	11.83	16.03	14	0.530	0.303
Late morning							
Autogroom	7.32	5.66	5.04	5.03	14	0.851	0.205
Receive	0.23	0.45	0.49	0.68	11.9[a]	−0.887	0.197
Direct	1.13	1.84	1.18	1.45	14	−0.064	0.475
Mutual	0.71	1.84	0.46	1.48	14	0.512	0.309
Total	9.40	6.20	7.17	5.27	14	0.775	0.226
Early afternoon							
Autogroom	7.10	4.21	4.31	3.76	14	1.396	0.093
Receive	0.81	1.63	0.42	0.82	14	0.603	0.278
Direct	1.23	1.81	0.70	0.99	10.8[a]	0.714	0.246
Mutual	3.12	3.53	0.62	0.92	7.91[a]	1.936	0.045
Total	12.25	8.65	6.06	3.37	14	1.886	0.040
Late afternoon							
Autogroom	4.24	2.31	3.40	2.30	14	0.729	0.239
Receive	0.34	0.63	0.25	0.46	14	0.349	0.366
Direct	0.50	0.71	0.38	0.78	14	0.330	0.373
Mutual	1.18	1.23	0.34	0.64	14	1.746	0.052
Total	6.27	2.61	4.65	3.78	14	1.001	0.167

[a] Equal variances not assumed, corrected *t*-test used.

TABLE 9. Location of food items on the toothrow during processing

Loss status	Location of food item processing: Anterior	Posterior	Unknown	Total N
Loss	39% (n = 235)	28% (n = 165)	33% (n = 196)	596
No loss	45% (n = 264)	26% (n = 151)	30 % (n = 175)	590
χ^2 for all columns:				χ^2 = 3.46, P = 0.177
χ^2 for anterior and posterior categories:				χ^2 = 2.03, P = 0.154

TABLE 10. Location on the toothrow used to process tamarind fruit

Loss status	Location of food item processing: Anterior	Posterior	Unknown	Total N
Loss	1% (n = 2)	69% (n = 129)	30% (n = 56)	187
No loss	3% (n = 4)	69% (n = 104)	29% (n = 44)	152
χ^2 for all columns:				χ^2 = 1.16, P = 0.559
Fisher's exact test for anterior and posterior categories:				P = 0.256

forage for, and consume, food items discarded in BMSR camp trash while the majority of her social group rested approximately 75 m away. Remaining active while others rest therefore enhances access to critical, high-value resources otherwise difficult to obtain within a group or competitive-foraging context. Although tooth loss alone did not predict significantly higher frequencies for total feeding, foraging, and grooming, individuals with greater than 10% tooth loss demonstrated significantly higher frequencies of feeding, foraging and grooming, and lower frequencies of resting during the early afternoon. These data indicate that individuals with extensive tooth loss demonstrate compensatory feeding, foraging, and grooming while others remain inactive and provides strong evidence for increased feeding-related and grooming behaviors in compensation for reduced dental efficiency. As between-sample differences in these behaviors only become statistically significant when limited to individuals with extensive tooth loss, it is evident that low-level tooth loss does not impact behavior to the same extent as extensive tooth loss. The impact of tooth loss upon behavior is thus related not only to the presence of dental impairment, but increases in accordance to the severity of dental impairment. As ring-tailed lemurs commonly rest and/or sleep during the early afternoon (e.g., Sauther, 1992), it is notable that those with tooth loss or extensive tooth loss do not appear to alter their patterns of feeding and foraging throughout the day, but rather use the "resting" period to maintain high levels of foraging and feeding, and for grooming. These data highlight that compensatory behaviors are manifested in a manner coherent with meeting individual needs while simultaneously balancing demands imposed by living within a social group (see later discussion).

A trend towards higher frequencies of total grooming for individuals with tooth loss during the early afternoon suggests that individuals compensate for toothcomb damage-related reductions in grooming efficiency behav-

TABLE 11. Use of licking behavior during food processing

Loss status	Licking behavior present			Total *N*
	Yes	No	Unknown	
Loss	24% (n = 142)	41% (*n* = 243)	35% (*n* = 211)	596
No loss	15% (n = 89)	43% (*n* = 254)	42% (*n* = 247)	590
χ^2 for all columns:				$\chi^2 = 15.2, P < 0.001$
χ^2 for yes and no processing categories:				$\chi^2 = 10.0, P = 0.002$

TABLE 12. Use of licking behavior to process tamarind fruit

Loss status	Licking behavior present			Total *N*
	Yes	No	Unknown	
Loss	70% (*n* = 130)	6% (*n* = 12)	24% (*n* = 45)	187
No loss	47% (*n* = 71)	16% (*n* = 24)	38% (*n* = 57)	152
χ^2 for all columns:				$\chi^2 = 19.3, P < 0.001$
χ^2 for yes and no processing categories:				$\chi^2 = 12.5, P < 0.001$

TABLE 13. Average feeding bout length by food item type

Food type	Loss		No loss		*df*	*t*-Value	Sig. (*P* =)
	Time (s)	SD	Time (s)	SD			
Fruit	146	25.27	121	33.90	14	−1.659	0.060
Leaves	135	54.97	129	24.44	14	−0.320	0.375
Other	227	220.10	187	163.46	13	−0.403	0.347
Unknown	45	52.20	39	23.48	9	−0.243	0.407
Total	143	22.63	129	25.39	14	−0.161	0.133

iorally. Grooming is associated with the removal of ectoparasites and contributes positively to individual health (Junge and Sauther, 2006; Sauther et al., 2002, 2006). Toothcomb damage and wear are common among the BMSR ring-tailed lemurs (Fig. 7 [Sauther et al., 2002; Cuozzo and Sauther 2004, 2006a; Cuozzo and Yamashita, 2006]). Toothcomb wear occurs in several manners: 1) beginning on the mesial portion of the comb, with wear proceeding distally, often exceeding 50% of the total comb (Fig. 7b), and 2) interstitially, as repeated scraping of hair during grooming leads to increased space between the teeth. Individuals with toothcomb wear are clearly impeded during grooming. For example, it is common to observe matted hair that completely covers the worn toothcomb (Fig. 7c). These individuals therefore remain active not only to enhance foraging and feeding returns, but also to compensate for losses in grooming efficiency. Focal animals possessing toothcomb wear demonstrate significantly higher rates of overall mutual allogrooming than those without toothcomb wear, as well as trends towards higher rates of autogrooming and total grooming. This is a very clear example of how dental impairment leads to a behavioral adjustment.

High rates of mutual allogrooming demonstrate that ring-tailed lemurs utilize social behaviors to mitigate the impact of dental impairment. By grooming with individuals without toothcomb wear, these individuals may receive more efficient and effective ectoparasite removal. As individuals with toothcomb wear do not receive grooming at relatively higher rates, we hypothesize that these lemurs encourage social partners to direct grooming behavior through direct and immediate reciprocation. Although grooming received from individuals with toothcomb wear or loss is likely less efficient, it is plausible that social partners are willing to engage in mutual allogrooming as this behavior is often directed towards areas of the body inaccessible to autogrooming [e.g., neck and head, (Barton, 1985)]. Alternatively, these social partners simply may not monitor the effectiveness of grooming received from those with toothcomb wear or loss. As we did not record which social partner initiated grooming, and toothcomb wear statistics are not available for all individuals within each social group, we cannot assess if those with toothcomb wear preferentially seek out and initiate reciprocal grooming bouts with individuals with low toothcomb wear and loss. Ongoing research will allow examination and assessment of the form and frequency of such behaviors.

Ring-tailed lemurs with tooth loss alter their activity budget in a manner broadly consistent with that described by Logan and Sanson (2002a,b) for koalas (*Phascolarctos cinereus*) who demonstrate extensive tooth wear. In contrast to koalas which demonstrate solitary feeding and foraging patterns, ring-tailed lemurs modify their behaviors primarily during periods when other individuals demonstrate reduced activity. These observations are consistent with the hypothesis that ring-tailed lemurs must balance compensatory behaviors with constraints imposed by living in a social group. Although dentally impaired lemurs must balance compensatory behaviors with group living, observed patterns of allogrooming suggest that living in a social group confers advantages to these individuals in terms of ectoparasite removal. No support is present for broad alterations to total activity budget as we predicted. Support is, however, present for the hypothesis that individuals with tooth loss engage in increased feeding, foraging, and grooming during periods when individuals without tooth loss are inactive.

No significant between-group differences were found for toothrow position (anterior vs. posterior) used during food processing for either all food items or for tamarind fruit. Ring-tailed lemurs typically process large, mechanically-challenging food items upon the posterior dentition, while items such as small herbaceous leaves are processed anteriorly (Sauther et al., 2002; Yamashita, 2003). These findings do not support the hypothesis that lemurs with tooth loss differentially process mechanically-challenging food items upon the anterior dentition.

Individuals with tooth loss demonstrate significantly higher frequencies of licking for both total feeding bouts and for feeding bouts of tamarind fruit, suggesting this behavior is used to compensate for tooth loss. Licking potentially breaks down food items with the tongue rather than with the teeth and also deposit saliva, thereby both moistening and potentially initiating the chemical breakdown of food items. Licking may also soften food items, facilitating further dental breakdown. For tamarind, licking also facilitates the removal and swallowing of smaller portions of this large fruit. Although individuals both with and without tooth loss were observed to lick tamarinds frequently, significant between-group differences suggest individuals with tooth loss differentially use licking behavior to gain access to this key food item.

Feeding bout length did not differ significantly between the "loss" and "no loss" samples for any food item type. However, significant differences are present between the "no/low loss" and "heavy loss" samples for fruit feeding ($P = 0.033$) bout length. Consumption of tamarind fruit appears to be the source of this variation, with "loss" individuals demonstrating significantly longer tamarind feeding bout lengths (Table 15; Fig. 6). Longer tamarind feeding bouts suggest individuals with tooth loss process tamarind fruit less efficiently than do individuals without tooth loss. Individuals with tooth loss likely take longer to process each individual fruit, or may spend more time licking to break down pods once opened. Similar bout lengths between groups for *Enterospermum* fruit (a soft, small round fruit which is simply swallowed with minimum processing and is processed anteriorly) suggest individuals with tooth loss do not consume more tamarinds per bout, but are spending more time in processing behaviors.

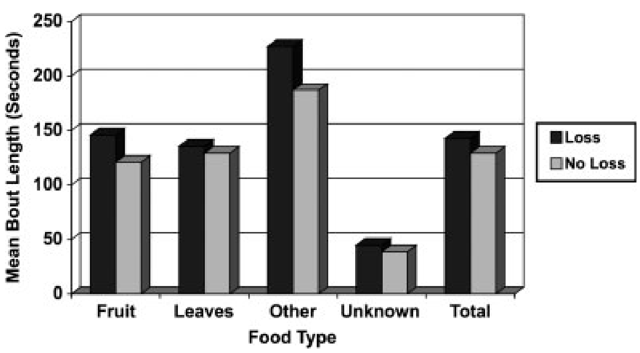

Fig. 5. Average feeding bout length by food item type and tooth loss status.

Individuals with tooth loss demonstrate a suite of behaviors uncommon among those lemurs without tooth loss and consistent with compensation for reduced dental function. These lemurs demonstrate behavioral responses to tooth loss primarily in terms of: 1) modifications to the activity budget during periods of group inactivity, and 2) use of licking to help process food items. They do not demonstrate higher overall rates for feeding or foraging, but do demonstrate evidence of reduced efficiency when processing difficult food items. Compensatory responses may therefore only partially mitigate the impact of tooth loss, particularly during the dry-season when tamarind fruit serves as a fallback resource (Cuozzo and Sauther, 2006a). Likewise, while dentally-impaired lemurs demonstrate divergent and apparently compensatory patterns of grooming, lemurs with tooth loss maintain relatively higher ectoparasite loads, suggesting this behavioral response is not fully compensatory (Sauther and Cuozzo, unpublished data). In terms of feeding behaviors, individuals with loss may also utilize behaviors not addressed by this study. Animals with tooth loss may selectively access food items with less-challenging mechanical properties than do individuals without tooth loss. Ring-tailed lemurs have also been observed to utilize food items pre-processed by other individuals, although the relationship of this behavior to dental impairment remains unclear (Cuozzo and Sauther, 2006a; Millette, unpublished data). Additionally, one individual (Blue 138) with extensive tooth loss (44%) has been repeatedly observed to process tamarind fruit manually by selecting fully ripe fruit, then using her hands to

TABLE 14. Average feeding bout length by heavy loss and no/low loss and food item type

	Heavy loss		No/low loss				
Food type	Time (s)	SD	Time (s)	SD	*df*	*t*-Value	Sig. ($P =$)
Fruit	150	24.5	121	31.7	14	2.010	0.033
Leaves	143	54.5	123	27.8	8.4[a]	0.882	0.201
Other	161	144.2	236	211.9	13	−0.760	0.231
Unknown	45	52.2	38	23.5	9	−0.243	0.407
Total	147	22.1	128	24.0	14	1.578	0.069

[a] Equal variances not assumed, corrected *t*-test used.

TABLE 15. Average feeding bout length for tamarinds and mantsaka fruit by tooth loss status

	Loss ($N = 8$)		No loss ($N = 8$)				
Food species	Time (s)	SD	Time (s)	SD	*df*	*t*-Value	Sig. ($P =$)
Tamarind	154	16.81	97	31.46	14	−4.348	<0.001
Mantsaka	172	118.04	164	92.77	14	−0.152	0.441

remove the hard outer shell (Sauther and Millette, personal observations; see Fig. 8). Further, some ring-tailed lemurs at BMSR engage in high rates of coprophagy, with individuals with tooth loss engaging in coprophagy at a higher rate than those without tooth loss. This may allow these individuals to access otherwise unavailable energetic and nutritional resources (Fish et al., 2007). The form and frequency of such behaviors among lemurs at BMSR, and the role these play as compensatory strategies is currently being assessed.

The magnitude with which tooth loss impacts dental function is presumably associated with the number of teeth absent from the dental arcade. Our data indicate that the form and frequency of compensatory behaviors varies between individuals with no or relatively minor tooth loss (e.g., <10%) and those with severe and extensive tooth loss (>10%). Although not assessed by this study, the location and severity of loss within specific areas of the dental arcade may also impact the expression of compensatory behaviors as ring-tailed lemurs utilize their anterior teeth primarily for food procurement (e.g., nipping), and grooming while posterior tooth positions are used primarily for mastication and processing of large and/or hard food items (Sauther et al., 2002; Yamashita, 2003). In this study, individuals with tooth loss rested significantly less during the early afternoon than did individuals without tooth loss. Trends towards increased grooming and foraging behaviors were observed among "loss" individuals, although no statistically definitive differences were observed. One explanation for these inconclusive findings is that individuals within the "loss" category demonstrate interindividual variation in loss between the anterior and postcanine dentition (see Table 1). Individuals with extensive tooth loss (or wear) of the anterior dentition may engage in relatively higher frequencies of grooming than those who demonstrate primarily postcanine loss. Individuals with predominantly postcanine loss may, in turn, primarily increase behaviors associated with consuming and breaking down food items. Our continued long-term study of the BMSR ring-tailed lemurs will provide additional information on the questions we address herein.

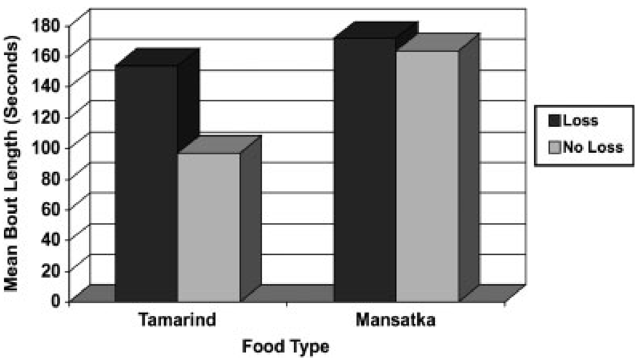

Fig. 6. Average feeding bout length for tamarind and mantsaka fruit by tooth loss status.

Implications for the evolution of human conspecific care

Antemortem tooth loss has played a central role in recent discussions concerning hominin conspecific care (Lebel et al., 2001; Lebel and Trinkaus, 2002; DeGusta 2002, 2003; Holden, 2003, Cuozzo and Sauther, 2004, 2006a; Lordkipanidze et al., 2006). Lebel et al. (2001) and Lebel and Trinkaus (2002) describe a Middle Pleistocene Neanderthal partial mandible (L'Aubesier 11) demonstrating $\geq$81.8% antemortem tooth loss. The remaining teeth in this specimen likely exhibit impairment as well (e.g., instability and/or malocclusion [Lebel et al., 2001; Lebel and Trinkaus, 2002]). Lordkipanidze et al. (2005, 2006) report extensive antemortem tooth loss (96.8%) in a 1.77 Mya Dmanisi *H. erectus* cranium and associated mandible (D3444/D3900). A central theme in the behavioral interpretation of these fossil hominins is the possibility that their continued survival required behavioral adaptations, specifically social assistance. Lordkipanidze et al. (2006) note that caution must be used when inferring behaviors among fossil hominins based on dental impairment, given their likely use of tools. Such caution is also noted in earlier work by Dettwyler (1991), and in DeGusta's critiques (2002, 2003), of interpreting behavior in fossil hominins, based on analyses of skeletal health, such as inferring conspecific care based

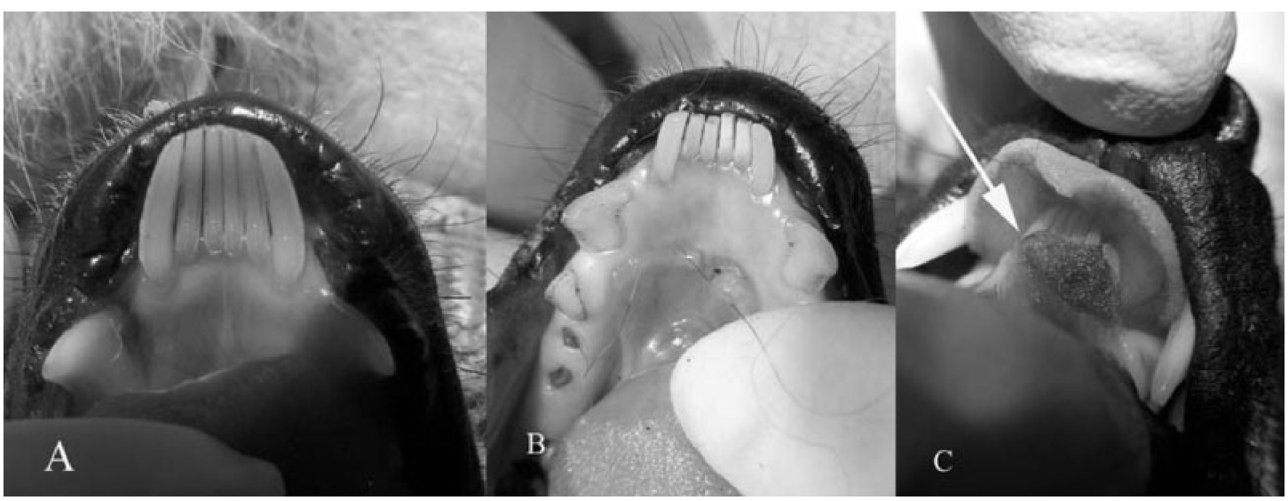

Fig. 7. Comparison of ring-tailed lemur toothcombs. (**a**) Unworn toothcomb; (**b**) heavily worn toothcomb; (**c**) worn toothcomb with hair matted into the comb. (Photo: M.L.S.).

Fig. 8. A ripe tamarind fruit processed using the hands. Note the complete removal of the mechanically challenging outer shell. (Photo: M.L.S.)

on antemortem tooth loss. Thus, new data presented in this article on behavioral responses to dental impairment among a population of extant primates allows us to further advance this discussion.

The data presented here indicate that ring-tailed lemurs compensate behaviorally for impaired masticatory ability without the presence of conspecific care. Here we highlight several potential alternative strategies by which early hominins may have compensated for tooth loss without invoking social assistance. As with ring-tailed lemurs, dentally-impaired hominins may have demonstrated 1) alterations to their activity budgets or 2) alternative food processing techniques. Individuals with tooth loss likely spent relatively more time engaged in activities associated with processing and/or consuming food items than did those without tooth loss. Likewise, individuals with dental impairment may have required additional time to processes challenging food items prior to consumption and/or utilized nondental food processing techniques (e.g., tools). Although impaired *Lemur catta* compensate for tooth loss through increased rates of licking behavior, fossil hominins, particularly later forms, possessed food processing technologies, with individuals with tooth loss likely to have utilized tools to break down food items prior to ingestion.

Although individual ring-tailed lemurs with toothcomb wear were observed to engage in relatively higher rates of mutual allogrooming, we do not suggest this behavior represents conspecific care. In this study, individuals with toothcomb wear received grooming from a social partner in exchange for grooming directed towards that social partner. Although this behavior provides evidence that impaired individuals may benefit from living within a social group and may mitigate the impacts of dental impairment through social behaviors, we find no evidence for the presence of conspecific care.

CONCLUSION

A common assumption among dental researchers is that extensive tooth loss subsequently results in death (see discussion in Lucas, 2004). However, ring-tailed lemurs at BMSR demonstrate high rates of long-term survival following tooth loss (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a,b). Our new data suggest that ring-tailed lemurs, and potentially other primates, compensate for dental impairment through behavioral mechanisms. We thus conclude the following:

1. Individuals with tooth loss demonstrate compensatory alterations in activity consistent with restrictions imposed by living within a social group. Individuals with tooth loss engage in less resting behavior during the early afternoon, when they demonstrate trends towards higher frequencies of foraging and grooming. The severity of tooth loss may also play a critical role in the expression of compensatory behaviors as individuals with >10% tooth loss demonstrate significantly different patterns of feeding, foraging, grooming, and resting during the early afternoon in contrast to those with <10% tooth loss.
2. Individuals with tooth loss demonstrate significant differences in food processing. Licking behaviors play a key role in behavioral compensation for tooth loss, particularly for tamarind fruit.
3. Behavioral responses examined in this study may not compensate fully for tooth loss, although individuals likely use alternative compensatory strategies that have not yet been fully addressed. Future research is required to assess how such behaviors may attenuate the effects of tooth loss.
4. Compensatory behaviors demonstrated by *Lemur catta* at BMSR may be analogous to those utilized by fossil hominins with tooth loss. We pose these behaviors as alternatives to conspecific care-based models for the extended survival of fossil hominins with extensive tooth loss.

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