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RESEARCH ARTICLE

A Comparison of Salivary pH in Sympatric Wild Lemurs (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar

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Chemical deterioration of teeth is common among modern humans, and has been suggested for some extinct primates. Dental erosion caused by acidic foods may also obscure microwear signals of mechanical food properties. Ring-tailed lemurs at the Beza Mahafaly Special Reserve (BMSR), Madagascar, display frequent severe tooth wear and subsequent tooth loss. In contrast, sympatric Verreaux's sifaka display far less tooth wear and infrequent tooth loss, despite both species regularly consuming acidic tamarind fruit. We investigated the potential impact of dietary acidity on tooth wear, collecting data on salivary pH from both species, as well as salivary pH from ring-tailed lemurs at Tsimanampesotse National Park, Madagascar. We also collected salivary pH data from ring-tailed lemurs at the Indianapolis Zoo, none of which had eaten for at least 12 hr before data collection. Mean salivary pH for the BMSR ring-tailed lemurs (8.098, $n = 41$, SD = 0.550) was significantly more alkaline than Verreaux's sifaka (7.481, $n = 26$, SD = 0.458). The mean salivary pH of BMSR (8.098) and Tsimanampesotse (8.080, $n = 25$, SD = 0.746) ring-tailed lemurs did not differ significantly. Salivary pH for the Indianapolis Zoo sample (8.125, $n = 16$, SD = 0.289) did not differ significantly from either the BMSR or Tsimanampesotse ring-tailed lemurs, but was significantly more alkaline than the BMSR Verreaux's sifaka sample. Regardless of the time between feeding and collection of pH data (from several minutes to nearly 1 hr), salivary pH for each wild lemur was above the "critical" pH of 5.5, below which enamel demineralization occurs. Thus, the high pH of lemur saliva suggests a strong buffering capacity, indicating the impact of acidic foods on dental wear is short-lived, likely having a limited effect. However, tannins in tamarind fruit may increase friction between teeth, thereby increasing attrition and wear in lemurs. These data also suggest that salivary pH varies between lemur species, corresponding to broad dietary categories. Am. J. Primatol. 70:363–371, 2008.

Key words: dental erosion; tooth wear; feeding ecology; dietary acidity; food chemistry; tannins

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INTRODUCTION

Tooth wear comes in a variety of forms including attrition, abrasion, and erosion [Gandara & Truelove, 1999; Hillson, 2005; Lucas, 2004; Shipley et al., 2005]. Erosion is the chemical deterioration of the dentition [e.g., Gandara & Truelove, 1999; Holt et al., 2000; Lucas, 2004; Lussi et al., 2004; Shipley et al., 2005], and occurs when acidity in the oral cavity falls below the ''critical'' pH level of 5.5, causing enamel demineralization [Newbrun, 1989; Shipley et al., 2005]. Chemical erosion of teeth is a major issue confronting modern humans, owing to a variety of dietary and behavioral causes, including gastrointestinal and eating disorders and the consumption of acidic foods [e.g., Gandara & Truelove, 1999; Holt et al., 2000; Lussi et al., 2004; Shipley et al., 2005; Verrett, 2001]. Continued erosion may lead to damage in the enamel, providing an opportunity for bacteria to invade the dental tissue [Frank, 1990]. Thus, the etiology of dental erosion is of great interest to dentists [e.g., Gandara & Truelove, 1999; Holt et al., 2000; Shipley et al., 2005]. Dental erosion may also compound analyses of dental microwear [e.g., Dumont, 1997]. Although a common tool when analyzing extant and fossil primates [see reviews in Teaford, 2000; Ungar, 1998, 2002], microwear data only reflect a short temporal frame [i.e., the ''last supper effect''; e.g., Grine et al., 2006], and may change markedly during the lifetime of an individual, possibly reflecting dietary changes as rapid as daily or seasonal variation [e.g., Hillson, 2005; Rafferty et al., 2002; Teaford and Tylenda, 1991]. Thus, dental erosion may obscure microwear signals. Acidity of food alone is not predictive of dental erosion [e.g., Lussi et al., 2004; Shipley et al., 2005], as saliva [primarily due to its bicarbonate content ;Gandara & Truelove, 1999; Newbrun, 1989] likely buffers the impact of acidic foods, thereby reducing demineralization and tissue loss [Dumont, 1997; Lucas, 2004; Newbrun, 1989; Shipley et al., 2005]. To date, data on natural variation in salivary pH have been published for a few non-human mammals [for extensive data on chiropterans, see Dumont, 1997].

Ring-tailed lemurs (*Lemur catta*) living in the gallery forests of the Beza Mahafaly Special Reserve (BMSR), Madagascar, exhibit high frequencies of severe, gross (i.e., macro) tooth wear (see Fig. 1a, an adult ring-tailed lemur skull from BMSR). They also exhibit high levels of antemortem tooth loss [26.5% of the population have lost at least one tooth and several individuals display over 80% tooth loss; Cuozzo & Sauther, 2006b; Sauther, et al., 2002]. In contrast, sympatric Verreaux's sifaka (*Propithecus verreauxi*) exhibit far less wear (see Fig. 1b, an adult Verreaux's sifaka skull from BMSR) and rare tooth loss [only 5.5% of the Verreaux's sifaka sample displayed tooth loss, with each example having lost only one tooth; Cuozzo & Sauther, 2006b]. Recently, chemical erosion resulting from the consumption of acidic fruits has been suggested as the cause of noticeable gross tooth wear in the extinct lemur *Pachylemur* [e.g., Godfrey et al., 2006; Vasey et al., 2005], the lone fossil representative of the lemurid family to which *L. catta* belongs [e.g., Godfrey & Jungers, 2002]. Thus, dental erosion may contribute to the pattern of gross tooth wear seen in the BMSR gallery forest ring-tailed lemurs, given their reliance on tamarind fruit [*Tamarindus indica*; e.g., Cuozzo & Sauther, 2006b; Sauther, 1998; Yamashita, 2002], an extremely acidic food [Table I; see also Gunasena & Hughes, 2000; Khandare et al., 2000; Pino et al., 2004]. Cuozzo and Sauther [2006b] suggested that, despite its high acidity [which does not change as the fruit ripens; Gunasena & Hughes, 2000; Table I], differences in the frequency of severe tooth wear and tooth loss between sympatric Verreaux's sifaka and ring-tailed lemurs are more likely a result of the mechanical properties of tamarind fruit. Specifically, despite both species often consuming this acidic food [Sauther, 1998; Yamashita, 2002], and both species possessing thin dental enamel [e.g., Godfrey et al., 2005], ring-tailed lemurs more often rely on hard

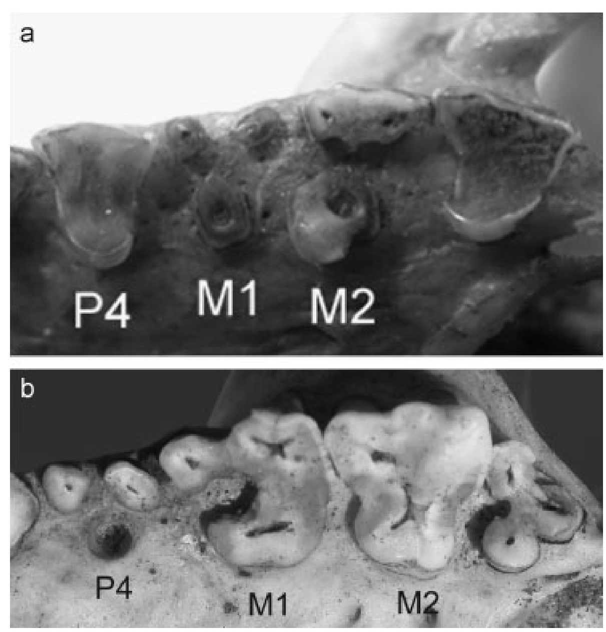

Fig. 1. (**a**) Severe tooth wear of the right maxillary teeth in the skull of an adult wild ring-tailed lemur from the Beza Mahafaly Special Reserve (BMSR) (Beza Mahafaly Osteological Collection(BMOC) 67). The degree of wear in this ring-tailed lemur specimen is moderate when compared with other BMOC and living BMSR ring-tailed lemurs [see figures in Cuozzo & Sauther, 2004, 2006b]. (**b**) Tooth wear of the right maxillary teeth in the skull of an adult wild Verreaux's sifaka from the BMSR (BMOC 163). Degree of wear in this specimen is the most advanced in the BMOC sifaka sample; note that the crowns of M1 and M2 in the sifaka remain intact, in contrast to those of *Lemur catta*. The degree of wear in the sifaka P4 is the only tooth in the sample ($n = 81$) that resembles the degree of wear common among ring-tailed lemurs. (a) and (b) are not to scale.

TABLE I. pH Values for Foods Eaten[a] by Ring-tailed Lemurs and Verreaux's Sifaka at the Beza Mahafaly Special Reserve

Plant	Portion	Mean pH (n)[b]	pH range
Lemur catta			
Tamarindus indica	Ripe fruit	2.34 (15)	1.60–3.80
Metaporana parvifolia	Mature leaves	5.00 (2)	4.70–5.30
Metaporana parvifolia	All leaves	5.00 (1)	NA
Azima tetracantha	Fruit	5.42 (4)	5.20–5.60
Goncrypta grevei	Mature leaves	5.50 (1)	NA
Marsdenia cordifolia	All leaves, stalk	5.63 (6)	5.00–6.60
Pentopetia grevei	All leaves	5.70 (1)	NA
Propithecus verreauxi			
Tamarindus indica	Unripe fruit	2.48 (6)	2.30–2.70
Tamarindus indica	Unripe fruit seed	4.00 (1)	NA
Terminalia mantali	Fruit	4.70 (1)	NA
Euphorbia tirucalli	Fruit	4.73 (4)	4.60–5.00
Euphorbia tirucalli	Young stalk latex	4.80 (18)	4.30–5.30
Marsdenia cordifolia	Mature leaves	5.40 (2)	5.40–5.40
Gonocrypta grevei	Mature leaves	5.50 (6)	5.00–6.50
Marsdenia cordifolia	Young leaves	5.80 (2)	5.70–5.90

NA, not available.
[a]The most frequently eaten food items based on time spent feeding by each lemur species [Yamashita, 2002].
[b]See text for discussion of pH measurement.

ripe fruit, whereas Verreaux's sifaka emphasize softer [although still quite tough; Yamashita, 2003], unripe fruit [Yamashita, 2000]. However, given the presence of a number of acidic foods in the diets of these two lemurs, especially tamarind fruit (see Table I), further exploration of the potential role of dietary acidity on their patterns of tooth wear is needed to systematically eliminate dental erosion as a cause of severe wear and tooth loss in BMSR ring-tailed lemurs.

Ring-tailed lemurs and Verreaux's sifaka at BMSR each eat a variety of foods yet exhibit distinct dietary patterns and behaviors. At BMSR adult Verreaux's sifaka weigh approximately 2,800 g [Richard et al., 2002], feed on a diverse diet of leaves, fruit, flowers, and bark, are primarily arboreal, and most live in groups of four to six individuals [Brockman & Whitten, 1996; Richard et al., 1993; Yamashita, 2002]. Verreaux's sifaka at BMSR emphasize a variety of leaves in their diets [Yamashita, 2002] and, like all sifaka species, exhibit a series of molar features that correspond to folivory [e.g., Seligsohn, 1977; Yamashita, 1998; see review in Cuozzo & Yamashita, 2006]. At BMSR adult ring-tailed lemurs average 2,100–2,400 g, depending on habitat [Sauther et al., 2006], live in large social groups of nine to 25 individuals [Sauther & Cuozzo, unpublished data], use all layers of the forest but are also significantly terrestrial, and exploit a wide variety of food resources including fruit, flowers, and leaves [Sauther et al., 1999]. *L. catta* teeth are far less derived than those of sifaka, although exhibiting some traits associated with folivory [e.g., Seligsohn, 1977; Yamashita, 1998]. However, the diet of *L. catta* at BMSR is dominated by tamarind fruit, a key fallback food given its asynchronous production and year-round availability [e.g., Cuozzo & Sauther, 2006a; Sauther, 1998; Yamashita, 2002]. Although dominated by leaves, the diet of Verreaux's sifaka at BMSR also includes the frequent consumption of unripe tamarind fruit [e.g., Yamashita, 2002].

The primary goal of our project is to further explore the potential impact of dietary acidity on lemur tooth wear. Using salivary pH data collected from wild ring-tailed lemurs and Verreaux's sifaka at BMSR, and from a second wild population of ring-tailed lemurs at Tsimanampesotse National Park, Madagascar, we assess the level of acidity in the oral cavity following feeding. One challenge we face while collecting data from endangered wild lemurs is the limited control over such variables as the length of time between feeding and data collection. To establish controlled, non-feeding salivary pH baseline values for ring-tailed lemurs, we collected salivary acidity data from the captive ring-tailed lemur troops at the Indianapolis Zoo, where data were collected following a minimum 12-hr fast as part of annual veterinary exams. We also present data on the acidity of foods eaten by ring-tailed lemurs and Verreaux's sifaka at BMSR.

Based on the variation in habitat and feeding ecology, particularly the relative presence of tamarind trees at BMSR and Tsimanampesotse, we expected:

(1) ring-tailed lemurs living in the tamarind-dominated gallery forest habitat at BMSR to have more acidic saliva values after feeding than the

ring-tailed lemurs at Tsimanampesotse, which is a varied habitat with few tamarind trees [Sauther & Cuozzo, 2008];
(2) sympatric BMSR gallery forest ring-tailed lemurs and Verreaux's sifaka to exhibit similar salivary pH following feeding, given the frequent consumption of tamarind fruit by both lemur species during the dry season when data were collected;
(3) the non-fasting BMSR gallery forest ring-tailed lemurs to exhibit more acidic saliva than the fasting Indianapolis Zoo ring-tailed lemurs, the latter representing salivary pH values with no immediate dietary influence.

Collecting data on acidity in the oral cavity will allow us to directly assess the potential role of dietary acidity as a cause of the high frequency of severe tooth wear and subsequent tooth loss in the BMSR ring-tailed lemurs [Cuozzo & Sauther, 2006b]. In addition, we provide the first comparison of salivary pH in sympatric lemurs, thus providing new information on possible differences in salivary pH related to diet, as seen in various chiropterans [Dumont, 1997].

METHODS

Samples and Localities

Between June and August 2006, we collected data on salivary pH from sympatric ring-tailed lemurs (*L. catta*, $n = 41$) and Verreaux's sifaka (*P. verreauxi*, $n = 26$) at the BMSR, southern Madagascar (23°30′S, 44°40′E). We also collected salivary pH data from 25 ring-tailed lemurs at Tsimanampesotse National Park, approximately 135 km southwest of BMSR, during May and June 2006. In December 2006, we collected salivary pH data from 16 ring-tailed lemurs at the Indianapolis Zoo, Indiana, USA, during annual veterinary exams. All *L. catta* and *P. verreauxi* pH data were collected from either subadults (i.e., 2nd-year individuals) or adults.

Lemur Anesthesia

Wild ring-tailed lemurs at BMSR and Tsimanampesotse 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 captures of ring-tailed lemurs at BMSR [e.g., Cuozzo & Sauther, 2006a,b; Sauther et al., 2002, 2006; Sussman, 1991]. Verreaux's sifaka were captured using a Telinject blow dart system (Telinject USA, Inc., Agua Dulce, CA) and Telazol®, based on protocols used over 20 years of study at BMSR [e.g., Lawler et al., 2005; Richard et al., 1993, 2002]. 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 data were collected, lemurs were placed in covered mesh cages and/or dog kennels, and kept in a quiet place for recovery. On recovery, individuals were released in the area from where they were originally captured (normally within 6 hr for ring-tailed lemurs; Verreaux's sifaka and several ring-tailed lemurs were released after a full night's recovery). Following standards outlined by the US CITES Management Authority (a unit of the US Fish and Wildlife Service), pH data were collected by a member of the research team (F.C.) wearing a protective surgical mask and gloves to preclude disease transfer while handling lemurs. All methods and materials received approval and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committees of the University of North Dakota, the University of Colorado, and the Boston University. Data collection in Madagascar was conducted with approval of the ANGAP (Association Nationale pour la Gestion des Aires Protégées), the body governing research in Madagascar's protected areas. Captive ring-tailed lemurs were anesthetized under manual restraint by facemask with isoflurane for their annual physical examinations. Once fully anesthetized, lemurs at the Indianapolis Zoo were intubated and maintained under anesthesia with isoflurane. Lemurs were given a complete physical examination, including weight, body temperature, and heart and respiratory rate. Anesthesia protocols followed industry standards, and were approved by the senior veterinarian. Anesthesia was administered by a licensed veterinarian or a veterinary technician under the supervision of a veterinarian.

Salivary pH

Salivary pH was recorded using Indigo Instruments' (Waterloo, Ontario Canada) wide, 1–14, pH paper. pH data were collected from wild lemurs and sifaka following their capture and transfer to field laboratories. Salivary pH data from wild lemurs were collected between several minutes to 1 hr after feeding, as all lemurs were feeding when initially anesthetized. pH data from captive lemurs were collected at a minimum of 12 hr after last feeding. Strips of pH paper were inserted into the oral cavity of each lemur for a total of 30 sec, first under the tongue, and then for an equal time between the mandibular gumline and the cheek. This ensured sufficient saliva to moisten the pH paper, and provided an overall oral cavity pH value. As salivary pH increases after exposure to air [Dumont, 1997], pH readings were recorded immediately after removal of the paper from the mouth, using color-coded scoring criteria. pH data were recorded as whole numbers, from one to 14. Individual lemurs whose color-coded values were intermediate between whole numbers were scored at intervals of 0.5.

Food pH

Lemur plant food pH at BMSR was collected by a member of the research team (N.Y.) in 1999–2000 as part of a comparative study of sifaka and ring-tailed lemur groups. Foods were tested using a handheld pH meter (Sentron, P.O. Box 125, 9300 AC Roden, The Netherlands). As most of the foods tested were fruits, juice was simply squeezed onto the sensor. Between tests the meter was rinsed off with bottled water and air-dried. At the beginning of each new batch of tests, the meter was calibrated with the buffers provided (pH 7.0 and 4.0). Foods tested were opportunistically discarded foods and selection of plant parts that were either near to where individual lemurs were feeding or foods that had actual bite marks. Approximately half the samples collected were from the ground and half from the tree (and branch if possible) where the lemurs were feeding.

Statistical Methods

Mean salivary pH between lemur samples was compared using an analysis of variance (ANOVA). Post hoc pairwise comparisons of variation between lemur samples were conducted with Fisher's protected least significant difference (PLSD). Mean pH between specific foods was compared using the Student's t-test. Significance level for all tests was set at $P = 0.05$. All data were analyzed using Statview data analysis software [Haycock et al., 1992].

RESULTS

Table I presents the mean pH of each of the most common foods, in terms of time spent feeding, eaten by ring-tailed lemurs and Verreaux's sifaka in each group studied at BMSR [Yamashita, 2002]. Among these food items, tamarind fruit (ripe and unripe) is the most acidic of all foods consumed by both lemur species. This includes the seeds of unripe fruit frequently eaten by Verreaux's sifaka. Tamarind fruit is also very acidic relative to fruits in general [e.g., Gunasena & Hughes, 2000; Khandare et al., 2000; Pino et al., 2004], with pH values for individual fruits at BMSR ranging as low as 1.60. These values are more acidic than many fruits and their products, such as lemon or lime juice [Gandara & Truelove, 1999], and approach the acidity of hydrochloric acid [Postlethwait & Hopson, 1992]. The mean salivary pH for each lemur sample is presented in Table II. The BMSR Verreaux's sifaka sample exhibits the lowest mean salivary pH (7.481, $n = 26$, SD = 0.458), whereas the Indianapolis Zoo ring-tailed lemur sample has the highest mean pH value (8.125, $n = 16$, SD = 0.289). As seen in Table II, salivary pH for individual lemurs ranges from 7 (neutral) to 9 (slightly alkaline) across the three ring-tailed lemur samples. As we expected an immediate dietary influence on salivary pH, this range is striking in that all ring-tailed lemurs examined, regardless of whether pH was recorded after feeding on acidic foods such as tamarind fruit (BMSR), or after a minimum of 12 hr of fasting (Indianapolis Zoo), exhibited neutral to slightly alkaline salivary pH, with no individuals having acidic saliva. This includes five individuals at BMSR that vomited (an occasional side effect of anesthesia) before the collection of salivary pH data. BMSR Verreaux's sifaka have a slightly more limited salivary pH range, from 7 to 8.5, but also have no individuals with acidic saliva despite having had their salivary pH tested after feeding. Of note, only one of the 26 sifaka had a salivary pH score of 8.5. Table III compares mean salivary pH between the different lemur samples. An ANOVA illustrates a difference between the four samples (ANOVA, $P < 0.0001$). BMSR *L. catta*, living in a tamarind-dominated gallery forest (mean pH = 8.098, $n = 41$, SD = 0.550), do not differ from Tsimanampesotse, a mixed habitat with few tamarind trees (mean pH = 8.080, $n = 25$, SD = 0.746; Fisher's PLSD, $P = 0.9009$), or the Indianapolis Zoo, a fasting, captive sample (mean pH = 8.125, $n = 16$, SD = 0.289; Fisher's PLSD, $P = 0.8669$). The Tsimanampesotse and Indianapolis Zoo *L. catta* samples also do not differ (Fisher's PLSD, $P = 0.8003$). In contrast, mean salivary pH for the BMSR Verreaux's sifaka sample (mean pH = 7.481, $n = 26$, SD = 0.458) is significantly less alkaline than

TABLE II. Salivary pH Values for Ring-tailed Lemurs at Beza Mahafaly Special Reserve, Tsimanampesotse National Park, and the Indianapolis Zoo, and Verreaux's Sifaka at Beza Mahafaly

Species	Location	n	Mean pH	pH range	SD
Lemur catta	BMSR	41	8.098	7.00–9.00	0.550
Lemur catta	Tsimanampesotse	25	8.080	7.00–9.00	0.746
Lemur catta	Indianapolis Zoo	16	8.125	8.00–9.00	0.289
Propithecus verreauxi	BMSR	26	7.481	7.00–8.50	0.458

BMSR, Beza Mahafaly Special Reserve.

TABLE III. Fisher's Protected Least Significant Difference Comparisons of Mean Salivary pH Between Lemur Samples

Comparison	Mean 1 (*n*)	Mean 2 (*n*)	*P*-value
BMSR *Lemur catta*, Indianapolis Zoo *Lemur catta*	8.098 (41)	8.125 (16)	0.8669
BMSR *Lemur catta*, Tsimanampesotse *Lemur catta*	8.098 (41)	8.080 (25)	0.9009
Indianapolis Zoo *Lemur catta*, Tsimanampesotse *Lemur catta*	8.125 (16)	8.080 (25)	0.8003
BMSR *Lemur catta*, BMSR *Propithecus verreauxi*	8.098 (41)	7.481 (26)	<0.0001
Indianapolis Zoo *Lemur catta*, BMSR *Propithecus verreauxi*	8.125 (16)	7.481 (26)	0.0004
Tsimanampesotse *Lemur catta*, BMSR *Propithecus verreauxi*	8.080 (25)	7.481 (26)	0.0002

BMSR, Beza Mahafaly Special Reserve.

the BMSR, Tsimanampesotse, and Indianapolis Zoo ring-tailed lemur samples (Fisher's PLSD, $P = <0.0001$, 0.0002, 0.0004, respectively).

DISCUSSION

Dietary Acidity and Dental Erosion

Chemical erosion of the dentition is common among modern humans, in part caused by consuming acidic foods [e.g., Gandara & Truelove, 1999; Holt et al., 2000; Shipley et al., 2005]. As many fruits and their juices are highly acidic [e.g., Gandara & Truelove, 1999], it is reasonable to expect that frugivorous mammals would exhibit a high frequency of dental erosion [Dumont, 1997]. In fact, some frugivorous bats do display dental erosion [Philips, 1971]. Recently, dental erosion has been suggested as a cause of gross tooth wear in the fossil lemur *Pachylemur* [Godfrey et al., 2006; Vasey et al., 2005], a lemur whose microwear patterns suggest a frugivorous diet [Godfrey et al., 2004]. However, as noted earlier, dietary acidity alone is not predictive of dental erosion [Shipley et al., 2005], in part because the bicarbonate content of saliva acts to buffer the acidity in foods [Gandara & Truelove, 1999; Newbrun, 1989]. Dumont [1997] suggested that frugivorous mammals may have high salivary pH to provide protection from dental erosion.

Given that the lemurs in our sample were frequently consuming acidic tamarind fruit [either the ripe fruit by ring-tailed lemurs or the seeds of unripe fruit, which are removed by sifaka using the toothcomb; Brockman, personal observation], we expected these individuals to exhibit acidic salivary pH, as data were collected soon after feeding. Thus, the absence of any individuals with a salivary pH value in the acidic range across both species at BMSR was unexpected (Table II). The fact that each of the five individual ring-tailed lemurs at BMSR that vomited following induction of anesthesia and before data collection had neutral or slightly alkaline salivary pH values is striking, as the continued presence of stomach acids (and other acidic fluids) in the oral cavity is a common cause of dental erosion in humans [e.g., Gandara & Truelove, 1999; Holt et al., 2000; Shipley et al., 2005]. Dental erosion occurs when acidity in the oral cavity falls below a ''critical'' pH of 5.5 [Newbrun, 1989; Shipley et al., 2005]. As neither population nor any individuals in our study exhibit a salivary pH below the ''critical'' 5.5 threshold after feeding, the acidity of tamarind fruit and other foods (see Table I) does not seem to contribute to the frequent severe wear and tooth loss in these ring-tailed lemurs.

Dental erosion is often diagnosed in humans by the presence of wear on the non-occluding surfaces [Gandara & Truelove, 1999] as well as a uniform pattern of wear throughout the dentition likely caused by the entire dentition being ''bathed'' by acidic fluids [see figures in Gandara & Truelove, 1999; Holt et al., 2000]. In both lemur species at BMSR, tooth wear, even when severe as in many ring-tailed lemurs [Cuozzo & Sauther, 2006a,b], occurs on the occluding surfaces. In addition, severe wear and tooth loss among the BMSR ring-tailed lemurs display a distinct pattern, corresponding to the tooth positions where tamarind fruit is initially processed, rather than uniformly throughout the mouth [Cuozzo & Sauther, 2006b]. When combined with the non-acidic salivary pH values in all individuals examined from both species, the pattern of wear seen primarily on the occluding surfaces eliminates dental erosion as the cause of severe tooth wear in the ring-tailed lemurs of BMSR.

We have argued previously that the pattern of gross tooth wear among the BMSR ring-tailed lemurs is primarily a product of the mechanical properties of frequently consumed tamarind fruit [e.g., Cuozzo & Sauther, 2006a], suggesting an incongruity between dental morphology and a frequently consumed food [Cuozzo & Sauther, 2006b]. Our new data eliminate dental erosion as a primary cause of this pattern. However, the chemical composition of tamarind fruit may indirectly impact ring-tailed lemur tooth wear at BMSR. Consumption of dietary tannins in mammals can be assessed by the presence of black stains on the teeth [Lucas, 2004]. At the BMSR, tamarind fruit contains five times the amount of tannins found in any other food

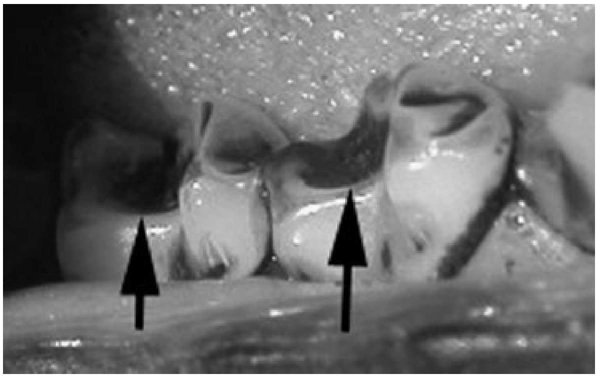

Fig. 2. Stained molar basins (M1 and M2, noted with black arrows) in a living, 4-year-old ring-tailed lemur (Orange 231) at Beza Mahafaly Special Reserve.

consumed by ring-tailed lemurs [Sauther & Ganzhorn, unpublished data] and often stains the teeth of BMSR ring-tailed lemurs [Cuozzo & Sauther, 2006b; Sauther et al., 2002; Fig. 2]. Dietary tannins reduce the lubricating qualities of saliva, increasing friction between teeth and thus dental attrition [Lucas, 2004; Prinz & Lucas, 2000]. Therefore, although the acidity of tamarind likely has a limited impact on lemur tooth wear at BMSR, given the apparent buffering capacity of saliva [which we plan to test directly, following Dumont, 1997], dietary tannins may contribute to the high frequency of severe wear and subsequent tooth loss among the BMSR ring-tailed lemurs. Such a pattern of wear and loss is not seen among the BMSR sifaka, despite the high level of tannins in their diet [Yamashita, in press]. This may relate to a higher percentage of tannin-binding salivary proteins found in a variety of mammals that regularly consume tannin-rich foods [see review in Clauss et al., 2005]. Along with a dental morphology adapted for their tough, leaf-dominated diet [Verreaux's sifaka have a tougher overall diet than do ring-tailed lemurs at BMSR; Yamashita, 2003], Verreaux's sifaka may possess tannin-binding salivary proteins, common to other browsing mammals [e.g., Clauss et al., 2005], thus reducing the influence of tannins on dental attrition but this remains to be determined for these species.

Salivary pH Variation and Feeding Ecology

Dumont [1997] noted that salivary pH reflects dietary habits, as insectivorous bats had significantly higher salivary pH than frugivorous taxa. Dumont [1997] also suggested that frugivorous mammals may possess high salivary pH to resist dental erosion caused by consuming acidic fruits. Thus, it is notable that the mean salivary pH values for all three ring-tailed lemur samples, despite the different characteristics of each (two wild samples, one from a tamarind-dominated forest, the other from a mixed habitat with few tamarind trees, and a fasting, captive sample), do not significantly differ. Dumont [1997] showed that salivary pH at feeding differed from salivary pH after fasting in a number of bat species. In contrast, as noted above and in Table III, there is no difference in mean salivary pH between the "at feeding" and "fasting" ring-tailed lemur samples. Thus, ring-tailed lemurs apparently have a mean salivary pH that is slightly alkaline (slightly >8) and significantly more alkaline than sympatric Verreaux's sifaka at BMSR. This appears related to differences in their diets.

At BMSR, ring-tailed lemurs have a more acidic diet than Verreaux's sifaka, largely influenced by their emphasis on tamarind fruit (see Table I). In four of the five groups studied by Yamashita [2002], ring-tailed lemurs spent over 30% of their time feeding on tamarind fruit. Tamarind leaves and unripe fruit are also common food resources of Verreaux's sifaka, but never exceeded 15% in any sifaka group studied in 1999–2000 [Yamashita, 2002]. A comparison of additional foods also illustrates the difference in dietary acidity between these two lemur species. *Euphorbia tirucalli* stalks, a dietary staple of Verreaux's sifaka despite its limited spatial distribution [Yamashita, 2002], is a food rarely eaten by ring-tailed lemurs [Sauther, 1992]. This food is significantly less acidic than tamarind fruit, the staple of ring-tailed lemurs (*E. tirucalli*, mean pH = 4.80, $n = 18$; *T. indica*, mean pH = 2.44, $n = 21$; $P = 0.0001$). The higher mean salivary pH of ring-tailed lemurs (Table III) may thus be a long-term response to a more acidic, frugivorous diet, and may in part allow the opportunistic exploitation of a variety of foods, despite some dental traits associated with folivory [Cuozzo & Sauther, 2006b; Seligsohn, 1977; Yamashita, 1998]. The similarity in salivary pH after feeding between the two wild ring-tailed lemur samples, which do not significantly differ from the fasting salivary pH of the Indianapolis Zoo sample, further suggests a species-specific value. In contrast, the salivary pH of Verreaux's sifaka is significantly closer to neutral (Table III), reflecting the dominance of a more folivorous diet, which is less acidic than the more frugivorous diet of sympatric ring-tailed lemurs (see Table I; see also the above data comparing *E. tirucalli* and *T. indica*). Our data on salivary pH and dietary acidity therefore support Dumont's [1997] suggestion that species-specific salivary pH values reflect dietary habits, indicating species-specific differences in digestive physiology. This corresponds to basic differences in the gastrointestinal tracts of ring-tailed lemurs and sifaka, the latter showing clear adaptations to folivory [Campbell et al., 2000], and provides an important area of further research. These results also indicate that salivary pH may be a useful tool in understanding sympatric primate species' dietary ecology.

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