Interpreting Food Processing Through Dietary Mechanical Properties: A *Lemur catta* Case Study

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ABSTRACT   Knowledge of dietary mechanical properties can be informative about physical consequences to consumers during ingestion and mastication. In this article, we examine how *Tamarindus indica* fruits can affect dental morphology in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly special reserve in southwestern Madagascar. Ring-tailed lemurs in tamarind dominated gallery forests exhibit extreme wear and tooth loss on their postcanine dentition that has been related to processing *T. indica* fruits. We measured and compared mechanical properties of individual food parts in the diet of ring-tailed lemurs in different seasons in 1999–2000, 2008, and 2010. Fracture toughness, hardness, and modulus of foods were measured with a portable mechanical tester. The ripe fruits of *T. indica* are indeed the toughest and hardest foods ingested by the lemurs. In addition, they are among the largest foods consumed, require high numbers of ingestive bites to process, and are the most frequently eaten by volume. During controlled cutting tests of the ripe fruit shell, multiple runaway side cracks form alongside the cut. Similarly, the lemurs repeatedly bite the ripe shell during feeding and thereby introduce multiple cracks that eventually fragment the shell. Studies of enamel microstructure (e.g., Lucas et al.: BioEssays 30 (2008) 374–385; Campbell et al., 2011) advance the idea that the thin enamel of ring-tailed lemur teeth is susceptible to substantial micro-cracking that rapidly erodes the teeth. We conclude that micro-cracking from repeated loads, in combination with the mechanical and physical properties of the fruit, is primarily responsible for the observed dental damage. Am J Phys Anthropol 148:205–214, 2012.   © 2012 Wiley Periodicals, Inc.

Knowledge of dietary mechanical properties can provide insights into behavioral approaches employed by non-human primates when procuring and ingesting foods (e.g., Lambert et al., 2004; Williams et al., 2005; Vogel et al., 2008; Wright et al., 2008; Wieczkowski, 2009; Yamashita et al., 2009). By extension, dietary properties can also be informative about physical consequences to consumers of particular foods during ingestion and mastication. In this article, we explore the physical connection between an observed feeding behavior and its potentially deleterious morphological consequences in a well-studied population of ring-tailed lemurs (*Lemur catta*). We describe how a pattern of extreme wear in this species directly reflects interaction with their environment.

Dental and general health of ring-tailed lemur individuals at Beza Mahafaly special reserve (BMSR) has been studied intensively since 2003. Cuozzo and Sauther (2004, 2006a,b) have documented multiple cases of extreme postcanine tooth wear and loss in lemur individuals, and posited that the lemurs' marked reliance on the ripe fruit of *Tamarindus indica* (kily) was the likely culprit (see Fig. 1). Of the 83 individuals sampled in 2003–2004, 26.5% showed some degree of tooth loss, a percentage only exceeded by *Gorilla gorilla* in a comparative sample of extant primates (Cuozzo and Sauther, 2006a). The majority of tooth loss occurred in a concentrated area from P3-M2 with the frequency of loss occurring in descending order from M1 to P4, (M_3), P3, and M2 (M^3 is not often lost). This does not coincide with the dental eruption sequence, which is M1, M2, P4, P3, P2, M3 (considering postcanines only). Cuozzo and Sauther (2006b) further noted that during feeding, the lemurs placed the large *T. indica* fruit pod on the post-canines precisely where extreme wear and tooth loss were observed, and speculated that the physical properties of the tamarind fruit were responsible for the damage to the postcanine toothrow.

In separate studies at the same site, Yamashita (2000, 2002, 2008) measured physical dietary properties of the foods of the two diurnal lemurs present, ring-tailed lemurs and sifakas (*Propithecus verreauxi*), and documented that the shell of the ripe *T. indica* fruit was the toughest and hardest plant part processed by the ring-tailed lemurs throughout the year. Although the fruit shell is not actually eaten, it is removed orally to expose the pulp underneath. Feeding on *T. indica* fruit proceeds

Fig. 1. Unripe *Tamarindus indica* fruit. Scale bar is in mm.

1999–2000, kily plant parts comprised 28.7% of the total time spent feeding by ring-tailed lemurs, of which 17.9% were ripe and unripe fruits. In contrast, the kily contribution to the annual diet of the sympatric sifaka was 11.7%, of which 4.7% were unripe fruit seeds and fruits (Yamashita, 2008a).

Given the importance of the fruit in the annual diet of ring-tailed lemurs, its site of initial placement on the postcanines, and its mechanical properties, *T. indica* fruit is most likely responsible for the extreme dental wear and loss patterns observed in ring-tailed lemurs at BMSR. In this article, we report on additional seasons of observations and mechanical testing of ring-tailed lemur diets at BMSR. Although a dietary study was conducted over the span of 13 months in 1999–2000, southwestern Madagascar is known for marked fluctuations in rainfall that can profoundly affect vegetative growth and food availability (Gould et al., 1999; Lawler et al., 2009). We therefore feel that it is important to continue to sample foods in later years. We address how *T. indica* fruits compare mechanically to other BMSR foods through multiple seasons and also compare them in terms of food size and time spent feeding on the most common foods. We conducted a detailed examination of breakage in *T. indica* fruit shell that parallels observed patterns of food processing behavior. Finally, we conclude with an exploration of possible relationships among enamel microstructure, fracture, and physical properties of *T. indica* fruits that could lead to the observed tooth damage.

MATERIALS AND METHODS
Study site and study species

We conducted feeding observations of the ring-tailed lemur, *Lemur catta*, in the deciduous tropical dry forest of Beza Mahafaly special reserve in southwestern Madagascar. Observations were conducted from February 1999 to February 2000, June 2008 (dry season), and January (wet season) and June–July 2010 (dry season).

The dry forest in this region has distinct wet and dry seasons. The rainy season, during which the majority of the annual rain falls, occurs approximately from November to March, and the dry season from April to October. The primary study site, Parcel 1 (80 ha), ranges from a tamarind dominated gallery forest in the east alongside a seasonal river to a dry, deciduous forest to the west (Sussman and Rakotozafy, 1994; Axel and Maurer, 2010). The parcel contains dense populations of two diurnal lemur species, *Lemur catta* and *Propithecus verreauxi* (Verreaux's sifaka) (e.g., Sauther, 1998; Richard et al., 2002). Lemur groups often range outside the fenced-in parcel into more degraded habitat surrounding the reserve, and some groups live exclusively in these disturbed areas.

Beginning in January 2010, observations were also conducted on ring-tailed lemur groups in the mixed forest (formerly known as Parcel 2) ~5 km west of Parcel 1 (Axel and Maurer, 2010). This forest is not enclosed and is interspersed with patches of dry, deciduous forest in our particular study area that resembles the western portion of Parcel 1 (Sussman et al., in press). Large areas of spiny vegetation dominate toward the south and southwest (Axel and Maurer, 2010).

Ring-tailed lemur group size ranged from 5 to over 15 individuals. Study groups were determined by location both inside and outside Parcel 1 in order to sample

in a stereotyped manner, where the whole fruit is inserted into the side of the mouth and bitten multiple times (e.g., Sauther et al., 2002; Yamashita, 2003; Cuozzo and Sauther, 2004, 2006). This initial placement of the fruit on the postcanines is largely dictated by its geometry (size and shape) (Yamashita, 2003). Food mass cannot be readily decoupled from toughness in terms of the site of ingestion. Large foods are almost always inserted into the side of the mouth regardless of their toughness values, and small foods are ingested anteriorly. Interestingly, dietary toughness for the two lemur species was not significantly different across the year, though the mechanical profiles of the contributing plant species differed. Whereas the ripe kily diet of ring-tailed lemurs was responsible for the high toughness of their diet, many plant species contributed to the toughest foods for sifakas. In terms of food hardness, ring-tailed lemurs swallowed much harder plant parts, principally seeds, than they masticated. The same pattern was true for sifakas; however, the hardness threshold, which demarcated when food parts were masticated or dropped, was significantly higher for sifakas than for ring-tailed lemurs (Yamashita, 2000).

Ring-tailed lemurs living in tamarind-dominated forests rely on the fruit of *T. indica* throughout the year (e.g., Sauther, 1998; Yamashita, 2002, 2008; Blumenfeld-Jones et al., 2006; Mertl-Millhollen et al., 2006; Simmen et al., 2006; Gemmill and Gould, 2008). At BMSR in

individuals in different microhabitats. Continuous bout, focal animal observations were facilitated by colored collars and numbered pendants. Focal animals were switched every 10 min (Altmann, 1974), or whenever an individual went out of sight. The groups in Parcel 2 were only partially habituated, so behavioral observations were conducted on general group movements instead of on a focal animal. In these cases, time spent feeding was measured from the time the animals entered a particular tree or feeding patch to the time they left.

During observations, we recorded time spent on feeding, movement, resting, and social activities. Feeding behaviors were further detailed by noting the plant species eaten, the exact part eaten (e.g., fruit pulp, etc.), food preparation techniques employed prior to biting off a section (often manual), and ingestive behaviors (initial placement and preparation in mouth prior to chewing). A feeding bout began when the focal individual manually or orally procured a food item and ended when the food was either dropped or the individual stopped eating for ~5 s.

Sample collection and mechanical tests

Foods were collected during observations and placed in Ziploc bags with a few drops of water to retain moisture. The majority of foods were either collected from the same plant as that observed eaten (collected foods often had bite marks) or were dropped by the animals when feeding in the canopy. Food samples were brought back to the field lab for testing at the end of the observation period. The portable mechanical tester used (Darvell et al., 1996) can be fitted for a number of different tests on its testing stage. Scissors toughness (R; fracture toughness with a scissors attachment), Vicker's hardness (H; indentation), and elastic modulus (E) in either compression or three-point bending were tested in this study. Fruit mesocarp and attached skin were separated from seeds for scissors testing since the ring-tailed lemurs generally do not masticate seeds. For those fruits in which the whole fruit was chewed (e.g., unripe *T. indica* fruit), the entire fruit was cut. For ripe *T. indica* fruit, the shell was the part tested in all mechanical tests. Not all plant parts were amenable to hardness tests (e.g., leaf material). Therefore, these tests were confined to fruits and seeds for the most part. Details on the operation of the tester can be found in Lucas (2004) and Yamashita et al. (2009). Briefly, load cells on the crosshead of the tester transmit force signals to an electronics box that integrates the signal and relays the information to an attached laptop computer. LabView software on the computer generates force-displacement graphs and returns values for the test being conducted.

Physical measurements (size and weight) of fruits including *T. indica* were also measured in the field. In addition, digitized photos were measured with the measurement tools in PhotoShop CS4.

Quantification of ingestive biting

Individuals were filmed *ad libitum* during feeding bouts with a handheld video camera (Sony Handycam with 20× optical zoom). Once the video was uploaded to a computer, we analyzed the video, which could be slowed down to 30 frames per second, and counted the numbers of bites taken to process a single fruit.
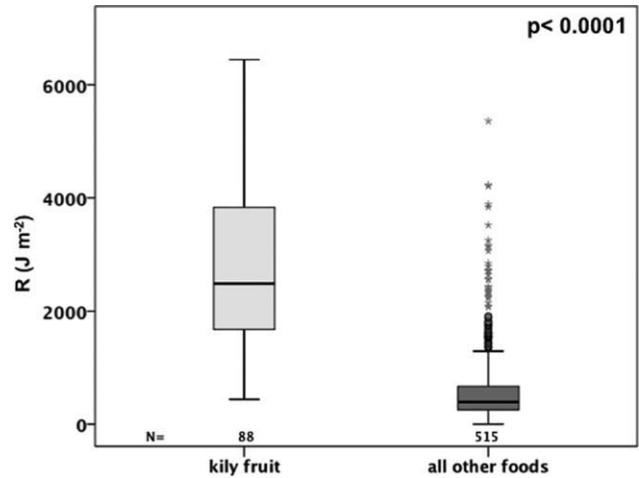

Fig. 2. Toughness comparisons of ripe and unripe *Tamarindus indica* fruits versus all other foods pooled across all seasons. Boxes represent the central half of the data; the median line bisects the box; whiskers, circles, and asterisks are data points that lie 1.5, 1.5–3, and >3 times, respectively, beyond the data range of the box.

"Bites" are defined as the numbers of times the jaws close on a food before biting off a mouth-size portion for chewing on the postcanines. Bites for each part per plant species were pooled and averaged.

Statistical analyses and data sets

Untransformed data were analyzed with nonparametric, Mann-Whitney U tests for comparisons of two samples and Kruskal-Wallis tests across multiple samples. Significance was set at $\alpha = 0.05$. We preferred nonparametric tests because the data were not normally distributed.

Datasets for mechanical tests were organized by year/season and by pooling all data for all years/seasons for each plant species tested. The data were initially separated by years to check for differences between the baseline 1999–2000 dataset and subsequent years.

RESULTS
Fracture toughness

Toughness values fluctuate significantly among seasons/years (Kruskal-Wallis $X^2 = 44.789$, $P < 0.0001$). Nevertheless, ripe *Tamarindus indica* fruit is the toughest component of the ring-tailed lemur diet and is highly significantly tougher than all non-*T. indica* foods (e.g., other fruits, leaf material, stalks) (Mann-Whitney U test: Z-score $= -13.104$; $P < 0.0001$) when data are pooled across all seasons (Fig. 2; Tables 1 and 2). Comparisons within each season are also significantly different at $P < 0.0001$. Ripe kily fruits are significantly tougher than unripe fruits when pooled across years (Mann-Whitney U test: Z-score $= -6.468$; $P < 0.0001$) (see Fig. 3).

Tables 1 and 2 provide results of mechanical tests and some metrics on *T. indica* fruit and other food items (principally fruits) in the ring-tailed lemur diet. As a note, modulus values are not included in Table 2, except for *T. indica*, because they were generally not tested for the foods included.

TABLE 1. Mechanical values and physical characteristics of Lemur catta *molars compared to* Tamarindus indica *fruit size*

	H^a (GPa)	E^a (GPa)	Length (mm)	Width (mm)
Enamel—OS[b]	4.54 GPa ± 0.17	87.12 GPa ± 1.14		
Enamel—EDJ[c]	4.43 GPa ± 0.00	88.27 GPa ± 0.45		
M^1 size[d]			4.89 (0.17)[e]	
M_1 size			5.18 (0.19)	
M^2 size			5.18 (0.14)	
M_2 size			5.58 (0.15)	
Ripe fruit[f]			64.99 (6)	21.79/14.82 (13)[g]
Unripe fruit			85.29 (4)	17.34/10.81 (35)[g]

[a] H, hardness; E, modulus.
[b] Values from Campbell et al. (this volume); OS, occlusal surface.
[c] Values from Campbell et al. (this volume); EDJ, enamel-dentine junction.
[d] Molar size values from Cuozzo and Sauther (2006b) for 2003–04.
[e] Values in parentheses for tooth lengths are standard deviations.
[f] All values are averages for each category across all years of testing.
[g] Width values are maximum/minimum; values in parentheses are numbers of individual fruits tested.

Indentation hardness

In 1999–2000, *T. indica* ripe and unripe fruits were not significantly different in hardness from plant parts, mostly seeds, which were swallowed but not masticated (Mann-Whitney *U* test: *Z*-score = −1.899; *P* = 0.058) [see also Yamashita (2000)]. Furthermore, ripe and unripe kily fruit hardnesses were not significantly different from each other (Mann-Whitney *U* test: *Z*-score = −1.149; *P* = 0.251). Likewise in 2008–2010, with additional plant species tested, plant parts that are swallowed are not significantly harder than masticated foods (M-W *U* test: *Z*-score = −1.382; *P* = 0.167). Of the foods that are chewed, however, kily fruits are significantly harder than other foods (M-W *U* test: *Z*-score = −4.642; *P* < 0.0001) (Fig. 4; Table 2).

Breakage profiles of *Tamarindus indica* fruit shell

Multiple side cracks form as the scissor blades close on a ripe *T. indica* fruit shell during a typical cutting test (see Fig. 5). From the force-displacement graphs of ripe and unripe kily fruit, it is clear that they have distinct toughness profiles (see Fig. 6). Ripe fruits are characterized by multiple cycles of peaks and drop-offs as the shell is cut and cracks form alongside the cut. Cracks propagate readily once started but require both high loads to initiate them and repeated loads for the shell to fall apart. Unripe fruit shell, on the other hand, behaves in a less brittle manner and displays none of the wide amplitudes seen in ripe fruit shell during the course of the cut. Cracks must be continuously driven in order to fracture the shell.

Ingestive behavior and feeding observations

Many bites are taken to process a single *Tamarindus indica* fruit compared to other select food items (Table 3). Small fruits, such as *Enterospermum pruinosum* (also see Table 2), require almost no preparation prior to mastication. Oral processing of bulky *Aloe* leaves is similar to *T. indica* fruits though aloe generally requires fewer ingestive bites and less time spent on single food items. Behaviorally, small and large food items are ingested differently. *E. pruinosum* is ingested at the front of the mouth by holding the fruit with the tongue against the palate and pulling the head back. Large foods such as *T. indica* (and aloe) are ingested on the postcanines. The lemur holds the ripe fruit in its hands, opens the mouth

wide, inserts the fruit into the side of the mouth on the postcanines, and bites it multiple times, often twisting it with the hands, until the pulp is exposed. The interior jelly is then scraped off by clamping the fruit between the teeth and pulling the fruit out with the hands. Lemurs will also often lick the interior. When eating unripe fruit, animals intersperse biting off small sections of the fruit with licking the exposed fruit and chewing the mouthful on the postcanines. When eating overripe fruit from the ground, the lemur places the fruit on the postcanines, closes the jaw, and pulls the fruit away with the hands to strip the pulp from the very tough threads (data not shown).

Time spent feeding on the top five foods for each observation season is presented in Table 4. Two months from the 1999–2000 study are shown that match seasons in later study periods. *T. indica* ripe and unripe fruits are consistently among the foods with the highest feeding times in each season.

DISCUSSION

Tamarindus indica fruit in context

Tamarindus indica fruit, especially the ripe fruit shell, is overall the toughest and hardest plant part fractured by the ring-tailed lemurs at BMSR (Tables 1 and 2). This is congruent with previous tests in 1999–2000 and is true across repeated sampled seasons. To put the ring-tailed lemur diet in a familiar context, the values for *T. indica* ripe fruit are roughly similar in toughness and modulus to popcorn kernels and fruit pits measured in Williams et al. (2005). Unripe fruits resemble cricket cuticles in toughness and apple pulp in modulus.

In terms of other metrics, *T. indica* fruits again stand out. They are among the largest individual food items consumed (Table 2), require the most time to process individually (Table 3), and are the most highly consumed foods in the ring-tailed lemur diet (Table 4). Their popularity despite their negative aspects is explained by their high glucose content (Yamashita, 2008b). All these variables point to the likelihood of this fruit being responsible for the heavy wear observed on ring-tailed lemur teeth.

As described elsewhere (Yamashita, 2002), toughness of the ripe *T. indica* shell is most likely overestimated. The many side-cracks attest to strain energy being diverted away from the scissors cut, and if the cut were not being controlled by the scissor blades, that would probably reduce toughness values (Figs. 5 and 6). A close

TABLE 2. *Physical measurements and mechanical properties of fruits in* Lemur catta *diet*[a]

Food species	Test date[b]	Plant part eaten	Length (mm)	Width[c] (mm)	Weight[c] (g)	H[d] (MPa)	R[d] (J m^{-2})	E[d] (MPa)
Aloe divaricata (aloe)	7/2010	Succulent leaf		38.70 (5)/ 7.66 (3)[e]		0.22 (3)	1533.10 (6)	
Anacolosa pervilleana (tanjaka)	1/2000, 1/2010	Ripe fruit	12.00 (6)	10.92 (7)	0.79 (3)		93.57 (3)	
Antidesma petiolare (voafogma)[f]	1/2010	Unripe fruit	12.20 (1)	13.36 (1)	1.14 (1)		603.20 (1)	
	2/2000	Ripe fruit	5.85 (2)	4.79 (2)	0.10 (2)			
Azima tetracantha (filoflo)	11/1999	Ripe fruit			0.10 (4)		248.28 (2)	
Crateva excelsa (akaly)[g]	1/2010	Unripe fruit	44.38 (1)	43.32 (1)	33.20 (1)		725.07 (5)	
Enterospermum pruinosum (mantsake)	5/1999, 6/2008, 6/2010	Ripe fruit	6.26 (2)	3.89 (2)	0.05 (2)		1465.90 (9)	
Grewia leucophylla (tratraborondreo)	3–4/1999	Unripe fruit	5.05 (3)	4.92 (3)	0.08 (1)		986.25 (1)	
Grewia sp. (malimatse)[f]	4–5/1999	Ripe fruit	8.53 (3)	11.33/6.02 (3)[h]	0.40 (3)			
Kalanchoe grandidieri (sofisofy)	7/2010	Succulent leaf				0.01 (1)	689.13 (2)	
Salvadora angustifolia (sasavy)	11/1999	Ripe fruit			0.23 (1)		503.25 (1)	
Strychnos madagascariensis (bakoa)	1/2010, 6/2010	Ripe fruit	29.42 (9)	29.43 (14)	15.89 (5)	0.23 (3)	2288.68 (10)	
Talinella grevei (dango)	1/2010	Ripe fruit	5.71 (2)	6.02 (2)	0.13 (2)		819.77 (6)	
Tamarindus indica (kily)[i]	1999–2000, 6/2008, 1/2010, 6–7/2010	Ripe fruit	64.99 (6)	21.79/14.82 (13)[h]	15.35 (3)	4.71 (6)	3371.97 (60)	418.27 (2)
Tamarindus indica (kily)	1999–2000, 6/2008, 1/2010, 6–7/2010	Unripe fruit	85.29 (4)	17.34/10.81 (35)[h]	10.85 (4)	1.99 (23)	1379.54 (28)	3.87 (4)
Terminalia fatraea (fatra)	2/2000						1365.90 (1)	
Kadidoka	7/2010	Ripe fruit	18.76 (1)	12.28 (2)	1.79 (1)	1.73 (2)	4599.83 (3)	
Rivervine	4–5/1999	Ripe fruit	13.77 (2)	12.94 (2)	1.34 (2)		638.08 (3)	
Sarirotsy	12/1999	Ripe fruit	35.09 (2)	9.38 (2)	2.34 (1)		917.07 (1)	
Sarisomangy	1/2010	Ripe fruit			1.93 (2)	0.28 (1)	676.20 (1)	
Sarisomangy	1/2010	Unripe fruit				0.56 (1)	743.40 (1)	
Saritoboara	4/1999	Ripe fruit	7.11 (2)	8.62 (2)	0.35 (2)		313.72 (2)	
Tsikembakemba	1/2010	Ripe fruit	3.93 (1)	4.55 (1)			131.87 (3)	
Tsiridambo	7/2010	Ripe fruit	34.89 (1)	9.25 (1)	1.18 (1)	0.42 (2)	1048.70 (2)	
Vahiranga	7/2010	Ripe fruit	47.51 (1)	11.30 (2)	4.34 (1)	0.01 (2)	1685.35 (2)	

[a] All values are averages for each category across all years of testing; numbers of individual fruits tested are in parentheses.
[b] Foods were tested when they were observed to be eaten; dates are month/year.
[c] Width values are maximum/minimum. Weight is wet weight in grams.
[d] H, hardness; E, modulus; R, toughness. The outer shell of the fruit was tested for hardness.
[e] Width at point of bite off/thickness of "leaf."
[f] No mechanical tests were conducted because the part eaten was a thin mesocarp scraped off a seed that was not chewed. The mesocarp could not be removed intact for mechanical tests.
[g] No mechanical tests were conducted because the fruit was dropped by the animal. Ripe fruits were eaten earlier.
[h] Maximum width/minimum width.
[i] *Tamarindus indica* ripe and unripe fruits were tested throughout February 1999–February 2000.
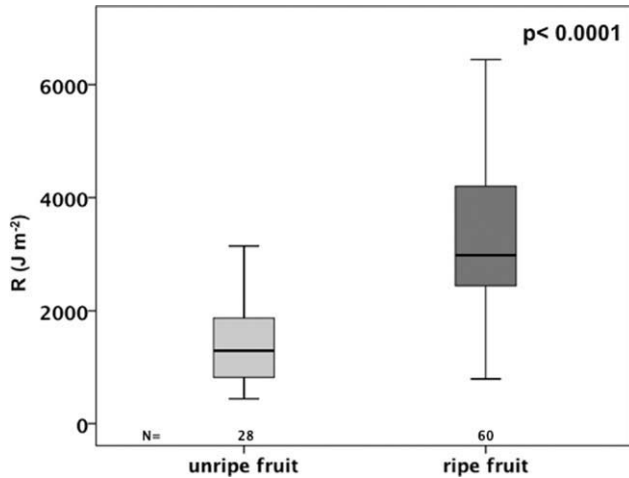
Fig. 3. Toughness values of ripe versus unripe *Tamarindus indica* fruit, pooled across years/seasons. See Figure 2 legend for explanation of symbols.
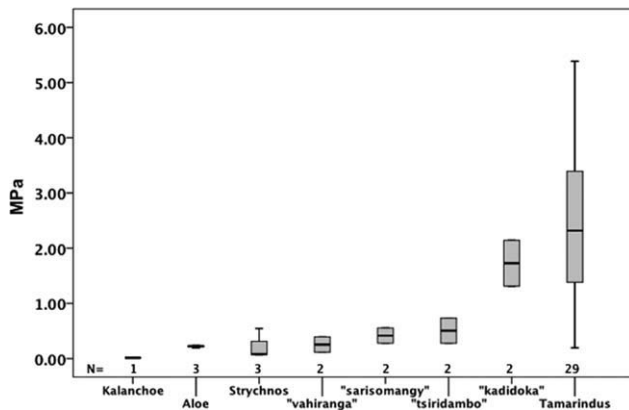

Fig. 5. Scissors cut of *Tamarindus indica* ripe fruit shell with side cracks. The straight edge of the scissor cut is along the lower margin with side cracks indicated by arrows. Scale is in mm. Thickness = 0.67 mm (for both ripe and unripe fruit shell; n = 2, 38, respectively).

Fig. 4. Hardness values of masticated foods. Plant parts that were swallowed without being chewed are not shown. Most foods tested are fruits, with some succulents (*Aloe, Kalanchoe*). Values for *Tamarindus indica* ripe and unripe fruits are pooled. Plant species are denoted by genus where known; vernacular names are in quotation marks. One *Tamarindus* extreme outlier is not shown, H = 7.09 MPa. *T. indica* fruits are harder than all other foods; Mann-Whitney U test: Z-score = −4.642; $P <$ 0.0001. See Figure 2 legend for explanation of symbols.

examination of this manner of breakage offers an explanation for the behavioral approach the lemurs take when eating kily fruits. Just as the scissor blades stress the ripe shell multiple times before it fragments, lemurs mimic the same process by repeatedly biting the fruit on the postcanines. High loads are applied and reapplied to start runaway cracks at each point until the shell fragments sufficiently to fall apart (Table 3).

Processing a single kily fruit requires many more bites than eating other fruits, which are generally much smaller (see Table 3) and are bitten off in one bite at the front of the mouth. Ingestive bites are even higher than for *Aloe*, which is processed in a similar manner. The difference is presumably related to differences in the mechanical properties of these two foods (Table 2). However, though kily fruit requires a relatively high degree of processing (ingestive bites per fruit are high), the
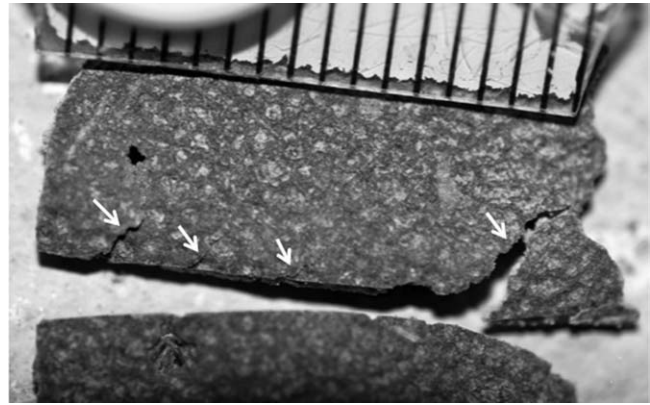
lemurs could potentially compensate for this by spending less time eating kily and more time on other foods. This does not appear to be the case. Even taking into account the processing time for a single fruit, the time spent feeding on kily is still much higher than for other foods (Table 4). A quick calculation demonstrates the difference: if we take the top two foods in 2008, *Enterospermum pruinosum* and *Tamarindus indica* fruits (ripe and unripe are pooled in this example), and divide the total feeding time for each species by the time it takes to consume one fruit, then the total fruits eaten for each species would be 7 h 2 min/1 s processing time (=25,320 individual fruits) for *E. pruinosum* and 6 h 11 min/1 min (=371 fruits) for *T. indica*. The average weight of *T. indica* fruit is ∼262 times that of *E. pruinosum* (13.1 g/0.05 g), yielding 69.94 *E. pruinosum* fruits on an equal volume basis to *T. indica* fruits (25,320/262). Clearly, the overall volume of kily fruit consumption is higher than for other foods.

The size of the *T. indica* fruit pod is large relative to ring-tailed lemur postcanine tooth size (Cuozzo and Sauther, 2006b) (Table 1). As described in Yamashita (2003), *T. indica* fruits are preferentially ingested on the postcanines rather than the anterior dentition. The enthusiasm of the ring-tailed lemurs for the fruit, despite the difficulties inherent in processing it, lends support to the hypothesis of a dental mismatch, where the teeth are not adapted to a primary fallback food (Sauther and Cuozzo, 2009). As described elsewhere (e. g., Yamashita, 1998), ring-tailed lemurs possess some of the morphologies associated with folivory such as relatively long molar crests and specialized digestive anatomy (sacculated cecum). In this, they converge with sympatric sifakas (*Propithecus verreauxi*), which are considered morphological folivores (Campbell et al., 2000; Cuozzo et al., 2008; Yamashita, 2008a). Furthermore, ring-tailed lemur dietary toughness is not significantly different from that of sifakas (Yamashita, 2008a).

The sifakas at BMSR suffer none of the extreme tooth wear incurred by ring-tailed lemurs (Cuozzo and Sauther, 2006a; Cuozzo et al., 2008). Though they also eat ripe kily fruit, they typically extract and consume the seeds from the unripe fruit (Yamashita, 2008a). Since unripe kily fruit is less tough than ripe fruit
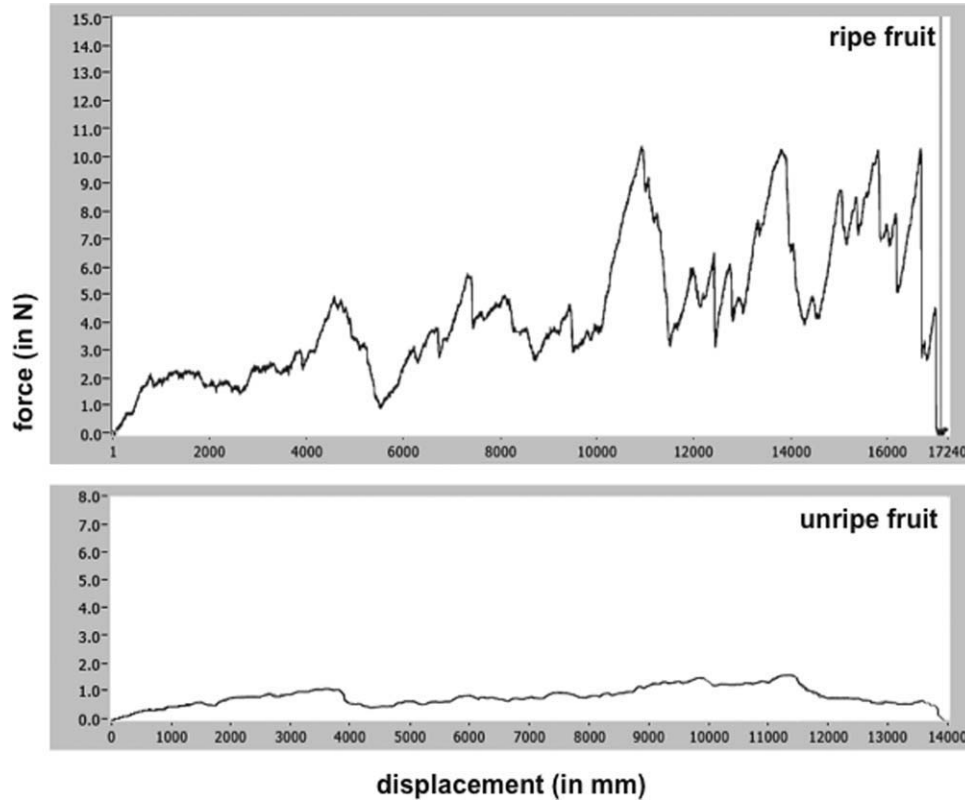
Fig. 6. LabView force-displacement graphs of ripe and unripe *Tamarindus indica* fruits. Ripe fruit (shell only), $R = 6445.2$ J m^{-2}; unripe fruit (shell only), $R = 1056.9$ J m^{-2} (average of 6 samples). Note multiple stress peaks on ripe fruit graph.

TABLE 3. *Ingestive biting counts for* Tamarindus indica *fruits compared to other foods*[a]

Food species	Food part	No. of bites[b] per single fruit (n)	Time to process[c] single food item (n)	Ingestive[d] location
Tamarindus indica (kily)	Old fruit[e]	14.2 (10)	55 s (9)	postcanines
Tamarindus indica (kily)	Unripe fruit	24 (3)	60 s (3)	postcanines
Enterospermum pruinosum (mantsake)[f]	Ripe fruit	1 (5)	<1 s (11)	anterior of mouth
Aloe divaricata[f]	Succulent leaf	15 (1)	60 s (1)	postcanines

[a] Bites were quantified by video analyses from 2008, 2010. "Bites" are numbers of times jaws close on food before biting off mouth-size portion for chewing on postcanines.
[b] Bites for each plant part were averaged for each plant species; numbers of bouts quantified are in parentheses.
[c] Time spent on each plant part was averaged for each plant species; numbers of individual fruits counted are in parentheses.
[d] "Ingestive location" refers to the location in the mouth where foods are first introduced. Ingestive behaviors are further described in the text.
[e] Old fruit are picked off the ground.
[f] These foods are included as a point of comparison to *T. indica* fruits. *Enterospermum pruinosum* is regularly eaten in large quantities in the dry season, and the size and ingestive location of *Aloe divaricata* is similar to *T. indica*.

(Fig. 3, Table 2), the lack of wear on sifaka teeth supports the hypothesis that it is the ripe kily fruit that largely contributes to the pattern of severe tooth wear in BMSR ring-tailed lemurs.

Tamarindus indica fruit and enamel loss

Lucas et al. (1994) measured mechanical properties of two seed species, *Macademia ternifolia* and *Mezzettia parviflora*, eaten by orangutans. *Macademia* seed shells fractured at a load of 1700 N (corresponding hardness values were 180 MPa for *Macademia* and 210 MPa for *Mezzettia*). The authors further speculated in Lucas et al. (2008) that sustained feeding even by orangutans on such foods may produce radial cracks [cracks radiating outward from the enamel-dentine junction (EDJ)] in the enamel that could be catastrophic. These cracks form when a stiff material such as enamel is loaded to the point that it produces tensile stresses in the more flexible underlying dentine (Lucas et al., 2008). Thick enamel, as found in orangutans and humans, protects the tooth from forming ra-

TABLE 4. Time spent feeding on top 5 foods in each season

Food species	Food part	Habit	% feeding time
May 1999[a]			
Tamarindus indica (kily)	Fruit (ripe)	Tree	0.25
Tamarindus indica (kily)	Flowers	Tree	0.17
Metaporana parvifolia (kililo)	All leaves	Vine	0.16
Rivervine	Ripe fruit	Vine	0.12
Latex vine	Mature leaves	Vine	0.09
January 2000[a]			
Tamarindus indica (kily)	Ripe fruit	Tree	0.18
	Unripe fruit	Tree	0.09
Marsdenia cordifolia (bokabe)	All leaves, tip	Vine	0.18
Talinella grevei (dango)	Stalk	Small tree	0.08
Metaporana parvifolia (kililo)	Young leaves	Vine	0.07
Misc. vines	All leaves	Vine	0.04
June 2008			
Enterospermum pruinosum (mantsake)	Ripe fruit	Shrub	0.45
Tamarindus indica (kily)	Ripe fruit	Tree	0.16
	Unripe fruit	Tree	0.23
Metaporana parvifolia (kililo)	All leaves	Vine	0.08
Salvadora angustifolia (sasavy)	Young leaves	Tree	0.03
Commicarpus commersonii (bea)	Mature leaves	Vine	0.02
January 2010			
Tamarindus indica (kily)	Ripe fruit	Tree	0.25
	Unripe fruit	Tree	0.02
Talinella grevei (dango)	Ripe fruit	Small tree	0.14
Metaporana parvifolia (kililo)	All leaves	Vine	0.07
Misc. ground vines	All leaves	Vine	0.06
Unknown vine	All leaves	Vine	0.06
June/July 2010			
Tamarindus indica (kily)	Ripe fruit	Tree	0.43
	Unripe fruit	Tree	0.24
Talinella grevei (dango)	All leaves	Small tree	0.17
Misc. vines	All leaves	Vine	0.05
Landolphia sp. (piravola)	All leaves	Vine	0.03
Metaporana parvifolia (kililo)	All leaves	Vine	0.02

[a] Months for 1999-2000 matched to seasons in later years.

dial cracks by limiting stresses to the surface where they are initially applied. Thin enamel would bend under sufficient loads and tense the underlying EDJ (Lucas et al., 2008).

Previously, Cuozzo and Sauther (2006a) noted the production of micro-cracks in ring-tailed lemur enamel that they speculated could lead to rapid macrowear. The rate of wear was so dramatic that entire crown portions can be lost from 1 year to the next. As further demonstrated by Campbell et al. (this volume), *Lemur catta* dental enamel on the mesial cusps of the M^2 shows excessive wear and micro-cracking compared to *Propithecus verreauxi* (Verreaux's sifaka) and *Lepilemur leucopus* (sportive lemur) molars. Whereas most microcracks were found near the EDJ in the sample as a whole, for *L.catta* cracking was also prevalent near the occlusal surface. *L. catta* teeth are so worn that the increase in hardness and modulus toward the enamel surface that characterizes the molars of the other lemur species is no longer

apparent. In addition, the lemurs sampled by Campbell et al. (2011) have relatively thin enamel compared to humans, and ring-tailed lemurs have the thinnest sampled. Sifakas compensate for their thin enamel with high decussation and sportive lemurs with large interprism areas, both of which increase enamel toughness. These findings strongly support the contention in Lucas et al. (2008) that thin enamel cannot adequately protect the tooth from the formation and proliferation of radial cracks when the tooth is stressed beyond a certain point. Constantino et al. (2009) further refine the argument to the size of the food item being an important determinant of the mode of fracture. *T. indica* fruits are large relative to tooth size (Table 1) and are thus expected to produce radial cracks as discussed above. In this case, the teeth do not so much "wear" as they fracture (Constantino et al., 2009).

While our data are not nearly as extreme as that found for orangutans, given the thin enamel of ring-tailed lemur teeth even the low values found for their more mechanically extreme foods appear sufficient to cause considerable dental damage. In addition, breaking apart ripe kily shell requires multiple loads, so sustained feeding behavior is an important contributing factor as predicted earlier by Lucas et al. (2008) for orangutans. From this, we can infer that ring-tailed lemur teeth can be worn by very low stresses, if those stresses are regularly applied. We offer hardness values as a point of comparison to orangutan seeds (we have no values for total load to fracture for whole fruits). Values as low as 7.09 MPa (highest value found for *T. indica* fruit shell) may be sufficient to cause extreme wear in the teeth of ring-tailed lemurs.

In summary, the mechanical and physical properties of *T. indica* fruit lead to a particular behavioral approach to processing it. Ingestion of the fruit on the postcanines involves multiple bites that coupled with the high frequency of the fruit in the diet repetitively stress the thin enamel. These repeated loads of a relatively large food item could induce the formation and proliferation of micro-cracks that radiate from the EDJ to the occlusal surface of the tooth, eventually producing the observed macrowear.

While it seems clear that *Tamarindus indica* fruit consumption is largely responsible for the wear observed in ring-tailed lemur teeth, other foods could also contribute. The leaves of the Mexican prickly poppy, *Argemone mexicana*, are processed in the same location on the toothrow as *T. indica* fruits and may also contribute to wear (Gemmill and Gould, 2008; Sauther and Cuozzo, 2009). Sauther and Cuozzo (2009) identified a characteristic wear pattern that occurred between the molars of individuals that foraged in the dry riverbed where *A. mexicana* grows during the dry season. The leaves of this plant also have silicates embedded in them that may scratch the teeth (Cuozzo et al., 2011). However, the pattern of severe wear and tooth loss in the BMSR ring-tailed lemurs transcends groups that feed on this introduced plant.

Aloe divaricata is also a food that has to be continuously bitten on the postcanines during pre-masticatory processing. However, its toughness and hardness values are lower than for ripe kily and it requires less ingestive bites (Tables 2 and 3). Furthermore, it, too, is limited in its distribution at the site (it is not found within the protected area of the reserve) and so is not a common resource for all ring-tailed lemur groups.

Finally, analyses of ontogenetic dental wear patterns are needed to assess the impact of such extreme wear and loss in this population of ring-tailed lemurs. Are functional edges maintained as wear progresses (as shown for rainforest sifakas in King et al., 2005)? Or, are the cusps blunted at early stages of wear? The appearance of wear in even young animals at BMSR (Sauther and Cuozzo, 2009) suggests that reliance on ripe kily fruit is contributing to accelerated dental senescence in this population of ring-tailed lemurs, which could affect other life history parameters (e.g., mortality, fecundity, etc.). King et al. (2005), for example, found a positive relationship between dental and reproductive senescence in a rainforest sifaka, *Propithecus edwardsi*. Preliminary results for the BMSR ringtailed lemurs, however, suggest that infant survivorship does not have a one-to-one correspondence with degree of wear and loss in this population, though this needs to be tested with a larger sample (Cuozzo et al., 2010).

SUMMARY AND CONCLUSIONS

The observed postcanine tooth wear in ring-tailed lemurs can be directly related to the toughness and hardness of the ripe *Tamarindus indica* fruit shell, which requires high and repeated loads to crack. During feeding, ring-tailed lemur individuals place the fruits on their postcanines and bite them repeatedly to initiate multiple runaway cracks that eventually fragment the ripe fruit shell. Such sustained loads on the teeth most likely produce microcracks radiating from the EDJ, which weaken the enamel and can lead to the rapid wear observed in this species. Ring-tailed lemur teeth in the tamarind-dominated forests of Beza Mahafaly are not well-suited to processing their most commonly eaten food.

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