

# Chapter 17

## Food Physical Properties and Their Relationship to Morphology: The Curious Case of *kily*

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### Contents

17.1	Background	387
17.2	Materials and Methods	390
17.2.1	Study Site and Species	390
17.2.2	Plant Collection and Mechanical Tests	390
17.2.3	Tooth Morphometrics	392
17.2.4	Analyses	393
17.3	Results	394
17.3.1	Kily Contribution to Lemur Diets	394
17.3.2	Mechanical Properties of Kily Plant Parts	395
17.3.3	Molar Morphometrics	398
17.4	Discussion	400
17.4.1	Comparisons of Tooth Features	400
17.4.2	Comparisons with Larger Diet	402
17.5	Conclusions	403
	References	404

### 17.1 Background

When diet is related to masticatory design, it is with reference to physical parameters of food items (e.g., Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Lucas, 1979; Hiiemae and Crompton, 1985; Happel, 1988; Kinzey and Norconk, 1990; Strait, 1993; Yamashita, 1998a; Wright, 2003). Functional dental morphology assumes a direct relationship between the external environment and the form that interacts with it. Physical interactions with foods, however, are just one parameter of the much broader issue of food choice. Herbivores must weigh nutritional benefits against the costs of eating specific parts. At the same time, the plant protects itself from being eaten (with the obvious exception of fruits) by

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manufacturing or possessing chemical or mechanical defenses to prevent herbivory. In terms of morphological interactions, the key defenses of concern are mechanical, and the ability of herbivorous species to overcome these defenses efficiently, by possessing appropriate morphological tools, determine in part the criterion for acceptance or rejection of particular plant parts.

Physical properties of foods are described in terms of external factors, such as size and shape, and internal properties that are related to the material composition of the particular food (see Strait, 1997; Lucas, 2004 for discussions). Food reduction depends on crack formation and propagation. The mechanical properties of the food in question describe its construction and determine how it resists crack propagation. *Toughness* is the work of fracture and is represented as the area underneath the curve in a force–displacement graph. Tough foods are good at stopping cracks once they start and are often able to undergo large deformations before they fail. *Brittleness* is its converse and is a relative lack of toughness. *Elastic* or *Young's modulus* is a measure of stiffness or resistance to bending. *Strength* at fracture is the force at which unrecoverable breakage occurs. *Hardness* is the resistance to indentation.

The relationship between two properties, toughness ( $R$ ), and elastic modulus ( $E$ ) describes how foods fragment and how they are used by plants to mount mechanical defenses against herbivory (Agrawal et al., 1998; Lucas et al., 2000; Lucas, 2004). The square root of the product of elastic modulus and toughness ( $\sqrt{ER}$ ) describes stress-limited defenses. Stress-limited foods are brittle and shatter when sufficient stress levels are reached. A plant that invests in this type of defense relies on an herbivore not being able to generate sufficient force to induce breakage. Displacement-limited defenses are represented by the square root of toughness divided by elastic modulus ( $\sqrt{R/E}$ ). These defenses rely on the herbivore not being able to strain the plant part to failure in order to fragment it (Agrawal et al., 1998). Thin sheets of material, such as leaves, tend to rely solely on toughness as a defense.

Mechanical plant defenses require appropriate tools to overcome them. Tooth features most suited for fragmenting foods with certain mechanical properties can be predicted based on engineering principles (Lucas, 2004). In earlier work, molar features were quantified and correlated with food properties for the lemurids (excluding *Hapalemur* spp.) and indriids (Yamashita, 1998a, b). Several functional complexes were identified: hard food items were correlated with short cusps in lemurids, tight occlusal fit, small trigon and large talonid areas, and deep, acute basins. Large, shallow trigons; shallow, unrestricted talonids; and large upper molar basins were indicative of a diet with high shear strength. The hardest and strongest foods eaten had higher correlations with tooth features than the most frequently eaten foods.

Tough foods (high in displacement-limited defenses) should require longer molar crests or blades with edges to cut them. The edges are necessary to continue and direct crack propagation to fragment the food. However, Yamashita (1998a, b) found that neither hardness nor shear strength demonstrated strong correlations with crest lengths, which were correlated with eating foods with a flat shape, such as leaves. Food toughness may have a more significant relationship.

Hard and/or brittle foods (low in displacement-limited defenses) should emphasize blunt cusps to propagate and drive cracks. The fit of occluding cusp/basin pairs

should be loose for tough foods to allow for greater excursions of the cusp and its adjacent crest to cut the food. Basins should be correspondingly unrestricted. Cusp height may increase as a means to increase crest length or overall tooth height (hypsodonty) as a defense against wear from abrasive diets.

Ecomorphological studies integrate ecology and functional morphology (Wainwright and Reilly, 1994). In this regard, identifying which dietary elements have the strongest correlations with the masticatory apparatus necessitates conducting mechanical tests in the field. In this study, I examine mechanical properties of a key resource in the diets of two Malagasy lemurs as an example of how diet and a particular aspect of the masticatory apparatus, tooth morphology, interrelate. *Lemur catta* (ringtailed lemur) and *Propithecus v. verreauxi* (white sifaka) differ markedly in behavior and morphology (Tattersall, 1982; Gebo, 1987; Richard et al., 1991; Sussman, 1991; Demes et al., 1996; Yamashita, 1998b; Richard et al., 2002; Gould et al., 2003).

At the site of Beza Mahafaly in southwestern Madagascar, the two species are sympatric and occur in high densities. The ringtailed lemur is a generalist herbivore that is frequently terrestrial (Sauter et al., 1999), and the sifaka is a folivore with complementary specialized morphology (e.g., spiral colon, sacculated cecum for housing bacterial symbionts for breaking down cellulose, highly crested molars) (Tattersall, 1982; Campbell et al., 2000).

In terms of masticatory morphology, lemurids as a family are more variable than indriids in molar crest length, tooth area, cusp radius and height, and basin areas (Yamashita, 1998a,b). Compared to lemurids, indriids are more dentally uniform, have notable molar crest development on quadritubercular teeth, fewer teeth, accelerated dental development, deep and robust jaws, and a partially fused symphysis (Beecher, 1977; Tattersall, 1982; Schwartz and Tattersall, 1985; Yamashita, 1998b; Godfrey et al., 2001, 2004).

Though there is a certain amount of dietary overlap, the lemur species eat plant parts from different phenophases (developmental stages) of a resource common to both their diets. *Tamarindus indica* (*kily*) is one of the most common trees in the shared forest habitat of the two lemur species (Sussman and Rakotozafy, 1994). At present, it is unknown whether *T. indica* is a native or an introduced species on the island (Binggeli, 2003). Regardless of its origins, it is well established in the dry forests of Madagascar. Its current distribution is pantropical (Missouri Botanical Garden, 2006). *T. indica* is a dietary staple for both lemur species throughout the year (Sauter, 1998; Yamashita, 2002). Mature and immature leaves, unripe and ripe fruits, seeds, and flowers are eaten as they become available. I concentrate on a single food resource in this chapter because of its prevalence in the diets of the lemur species. Furthermore, the partitioning of its various parts by the two lemurs appears to reflect larger patterns of food selection, which may indicate mechanical segregation. Tooth morphologies are predicted to be congruent with differences in the mechanical properties of the plant parts eaten. Specifically, in comparisons between the lemur species, longer tooth crests are expected to be correlated with tougher foods, blunt cusps with hard/brittle foods, looser occluding cusp/basin pairs with tougher foods, and unrestricted basins and higher cusps with tough foods.

## 17.2 Materials and Methods

### 17.2.1 Study Site and Species

Observations of *Propithecus v. verreauxi* and *Lemur catta* were conducted in the deciduous tropical dry forest of Beza Mahafaly special reserve in southwestern Madagascar from February 1999 to February 2000. This region is characterized by distinct wet and dry seasons. The majority of rainfall occurs between the rainy season months of November to March with almost no rain during the dry season approximately from April to October. The primary study site, Parcel 1, is a small (80 ha) area with a diversity of microhabitats ranging from a riverine gallery forest in the east to a xeric habitat to the west (Sussman and Rakotozafy, 1994). Parcel 1 contains dense populations of the two diurnal lemur species studied (Richard et al., 2002; Yamashita, 2002; Gould et al., 2003).

Five ringtailed lemur and six sifaka groups were observed. Ringtailed lemur groups contained from ten to more than fourteen individuals. Sifaka group sizes ranged from four to seven individuals. Identifying collars and pendants on individual animals facilitated focal observations. Continuous bout observations were conducted on focal animals that were changed every 10 min (Altmann, 1974). Time spent on basic behaviors of feeding, movement, resting, and social activities was recorded. Feeding behaviors were further detailed by noting the plant species eaten, the exact part eaten (e.g., young or mature leaves, fruit pulp, etc.), food preparation techniques employed, and ingestive behaviors.

Ringtailed lemurs and sifakas ate different developmental phases of specific kily parts throughout the year. Ripe kily fruits are pods with a brittle exocarp surrounding a jelly-like mesocarp. While both lemurs eat the ripe fruits, sifakas restrict ripe fruit eating to a few months at the end of the dry season. Ringtailed lemurs eat ripe fruit pulp throughout the year. Seeds from ripe fruit are not eaten by either species; sifakas, however, preferentially eat seeds from unripe fruits. The pinnate leaves flush bright pink and gradually expand and green as they mature. Ringtailed lemurs eat immature leaves, whereas sifakas concentrate on the more mature phase.

### 17.2.2 Plant Collection and Mechanical Tests

Food trees were flagged during observations for later plant part collection. In some cases, animals dropped foods that were collected at the time of observation. Foods were usually collected and tested on the same day as observations, or at least within 24 h. Care was taken to collect the exact plant part from the tree that the animals were observed feeding on. Many of the foods tested were either chewed and dropped by the animals or had adjacent bite marks. Specific *T. indica* parts that were eaten and collected included young and mature leaves, unripe fruit, exocarp of ripe fruit, seeds from unripe and ripe fruits, and flowers (Fig. 17.1).

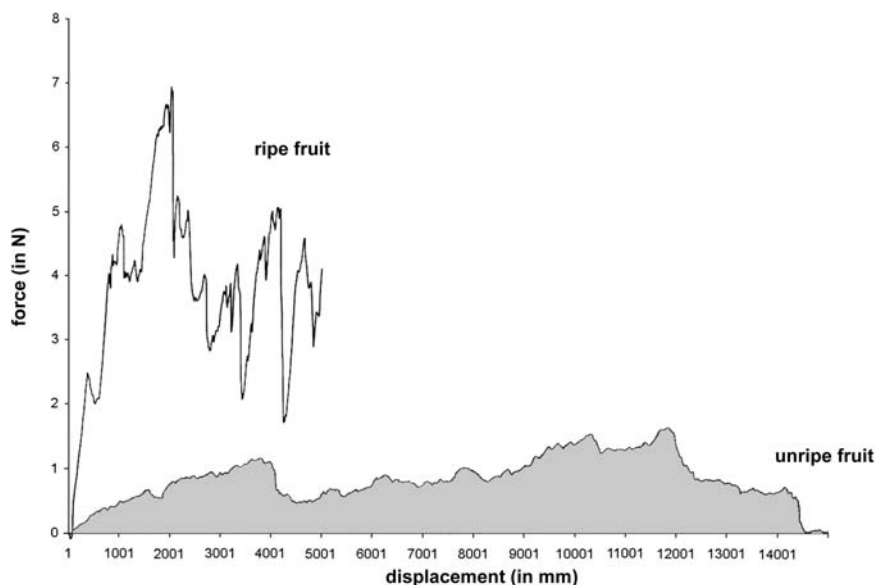


**Fig. 17.1** Unripe kily fruit and seeds dropped by sifakas. Coin diameter = 21 mm

Feeding observations focused on the specific point where foods were bitten off, and the toughness (in  $J/m^2$ ) of these plant parts was tested with a portable mechanical tester (Darvell et al., 1996; Lucas et al., 2000). The instrument has a number of interchangeable pieces that can be used to perform a variety of mechanical tests.

The toughness ( $R$ ) ( $J/m^2$ ) for most individual food parts was determined by a scissors cutting test. In the test, a platform with an attached load cell (either 10 or 100 N) is lowered onto the scissor handles. A controlled crack forms as the scissor blades close down on the food item. After the food is cut to a preset length, a second, empty pass of the scissor blades alone subtracts out the work of friction between the scissor blades. The output to a computer is a force–displacement diagram, such as the one in Fig. 17.2. Figure 17.2 depicts graphs of ripe and unripe *Tamarindus indica* fruit, where force is on the Y-axis and displacement is on the X-axis. The computer program returns toughness values in  $J m^{-2}$ , which is the area under the force–displacement curve (shaded area), or the work of fracture.

Fruits were tested according to the first part encountered, in most cases the fruit shell or fleshy mesocarp with attached exocarp. Scissors tests of ripe kily fruit shells were conducted by cutting small test pieces out of the shell. Bipinnate kily leaves were tested on the rachis or pinnae that support individual leaflets and through individual pinnules. In some cases where the pinnules were too delicate, rows of pinnules were stacked and cut together. Flowers were most often tested at the individual pedicel that supports the flower, and toughness of either individual flower parts (petals, sepals) or through the nectary was taken.



**Fig. 17.2** Force–displacement graph of scissors cutting test of ripe kily fruit shell and unripe kily fruit. Peaks in ripe fruit trace represent crack formation. Average toughness of all fruits tested: unripe fruit ( $R = 1199 \text{ J m}^{-2}$ ,  $n = 12$ ), ripe fruit ( $R = 3112 \text{ J m}^{-2}$ ,  $n = 24$ ). Figure adapted from Yamashita (2002; Fig. 17.2); used with the permission of Springer

Toughness was also measured with a wedge test, in which a wedge is lowered into a prepared block of food. Elastic modulus (in MPa) of kily fruit shell was tested in three-point bending. Hardness (in MPa) was tested with an indentation test in which a 1-mm ball bearing attached to the upper tester platform was pressed onto the food. The hardness sample comprised seeds and fruit casings (exocarps).

The numbers of times plants were tested are consistent with the numbers of observations of lemurs eating a specific plant part. Three to four individual parts were tested for each plant species each time the plant species was tested.

### 17.2.3 Tooth Morphometrics

Occlusal tooth areas, basin areas, crest lengths, radii of curvature of cusps, cusp heights, and ratios of occluding cusps and basins were measured from second upper and lower molars made from epoxy tooth casts of field and museum specimens (see Yamashita, 1998a for details). Second molars were chosen for study because of their intermediate position in the molar row.

Tooth features were measured with JAVA (Jandel Video Analysis software) and a Reflex microscope. Procedures and protocols are reported in Yamashita (1998a).

JAVA measures video images in two dimensions via either edge-tracking software that follows contours based on the contrast of the image or by tracing non-linear features manually from the keyboard. Teeth were oriented so that the plane of the occlusal surface of the second molar was parallel with the videocamera lens. Molar crown areas and basin areas were measured in millimeter square with JAVA.

Indriids and lemurids differ in the presence of some basins. Both families have an upper molar trigon and lower molar trigonid and talonid; however, the trigonid in lemurids does not occlude with an upper molar cusp. The indriid quadritubercular molar has both a talon and a trigonid basin. Areas of the occlusal surfaces of upper and lower second molars were digitized in the same orientation as the basins. Two occlusal cusp/basin pairs, the protocone/talonid and hypoconid/trigon, were measured in both lemur taxa.

Measurements in three dimensions were obtained with a Reflex microscope. A high-intensity LED point acts as the measuring mark at the center of the microscope view. The microscope digitizes 3D coordinate data of the object of interest. Crest lengths, cusp heights, and cusp radii were measured with the Reflex scope. (See Yamashita, 1998a for details on specific measurements).

### 17.2.4 Analyses

Tooth features were compared using residuals from least squares regression analyses of individual features regressed separately against lower molar area within each family (Lemuridae and Indriidae; Table 17.1). Analyses were confined to residuals

**Table 17.1** Lemur species included in regressions

Taxa	Sample size <sup>a</sup>
Lemuridae	
<i>Lemur catta</i>	24
<i>Eulemur coronatus</i>	10
<i>E. fulvus albocollaris</i>	3
<i>E. fulvus albifrons</i>	10
<i>E. fulvus collaris</i>	8
<i>E. fulvus fulvus</i>	10
<i>E. fulvus mayottensis</i>	10
<i>E. fulvus rufus</i>	15 [2]
<i>E. fulvus sanfordi</i>	3
<i>E. macaco flavifrons</i>	2
<i>E. macaco macaco</i>	7
<i>E. mongoz</i>	10
<i>E. rubriventer</i>	24 [4]
<i>Varecia variegata rubra</i>	4
<i>V. variegata variegata</i>	6

(Continued)

**Table 17.1** (Continued)

Taxa	Sample size <sup>a</sup>
Indriidae	
<i>Avahi laniger laniger</i>	10
<i>Indri indri</i>	10
<i>Propithecus diadema candidus</i>	7
<i>P. diadema diadema</i>	8 [2]
<i>P. diadema edwardsi</i>	10 [9]
<i>P. diadema holomelas</i>	3
<i>P. verreauxi coquereli</i>	10
<i>P. verreauxi coronatus</i>	8
<i>P. verreauxi deckeni</i>	10
<i>P. verreauxi verreauxi</i>	25 [1]

<sup>a</sup> Numbers in brackets are field specimens.

since earlier analyses of covariance showed that, though the slopes of the two families do not differ significantly from isometry, the indriid intercept is significantly higher than that of the lemurids (Yamashita, 1998b). The dental samples, from museum and field collections, often did not have associated body weights and so required size surrogates for all regression analyses. Lower molar area was found to be a more appropriate size surrogate for comparisons than skull length in Yamashita (1998b).

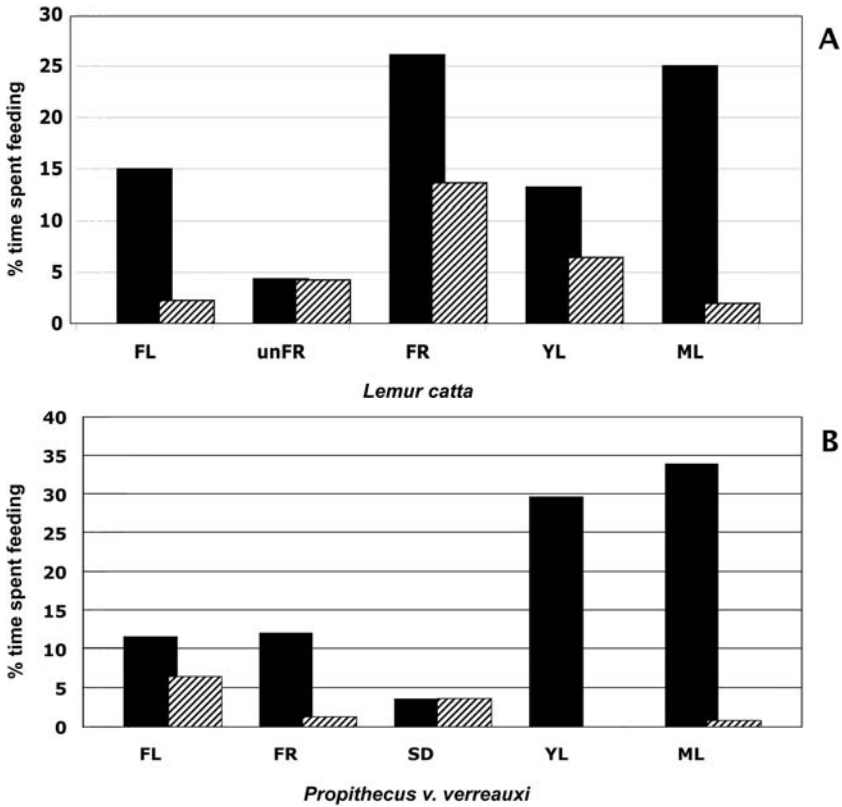
Raw data values were compared with non-parametric Mann-Whitney U and Kruskal-Wallis tests for all data sets comparing food properties. Tooth features were compared with non-parametric Mann-Whitney U tests on residuals derived from least squares regressions of individual tooth features against lower molar area within each family. However, raw data values were used for comparisons of cusp/basin ratios. Due to small sample sizes in some comparisons, results must be interpreted cautiously.

## 17.3 Results

### 17.3.1 Kily Contribution to Lemur Diets

*T. indica* fruit parts were eaten year-round and contributed to the diets of both lemur species, but especially to the diets of the ringtailed lemurs (Fig. 17.3). Ringtailed lemurs spent 29% of total annual feeding time on various kily plant parts (ripe and unripe fruits, flowers, and young leaves). Sifakas spent 11% of total feeding time on flowers, unripe fruit seeds, ripe fruits, and mature leaves.



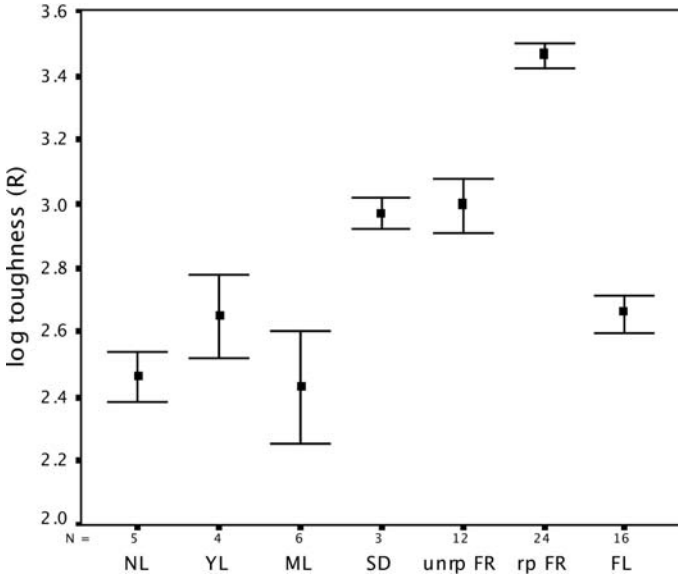


**Fig. 17.3** Time spent feeding on kily parts throughout year compared to total annual feeding time on same food parts. Food categories of total diet confined to match categories of kily plant parts eaten. (A) *Lemur catta*; (B) *Propithecus v. verreauxi*. Solid bars, total annual diet; cross-hatched bars, kily diet expressed as percentage of total diet. FL = flowers; unrp FR, unripe fruit; FR pulp, ripe fruit pulp; SD, unripe fruit seed; YL, young leaves; ML, mature leaves. No kily YL parts for sifakas

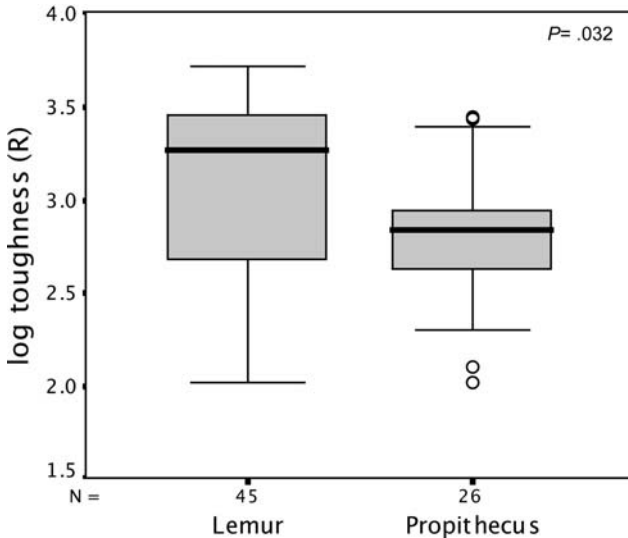
### 17.3.2 Mechanical Properties of Kily Plant Parts

Toughnesses of different kily plant parts were mechanically distinct from one another (Kruskal-Wallis  $\chi^2 = 42.547$ ,  $P < 0.0001$ ; Figs. 17.2, 17.4). Average toughness values for all fruits tested in Fig. 17.2 were: unripe fruit ( $R = 1199 \text{ J m}^{-2}$ ,  $n = 12$ ) and ripe fruit ( $R = 3112 \text{ J m}^{-2}$ ,  $n = 24$ ).

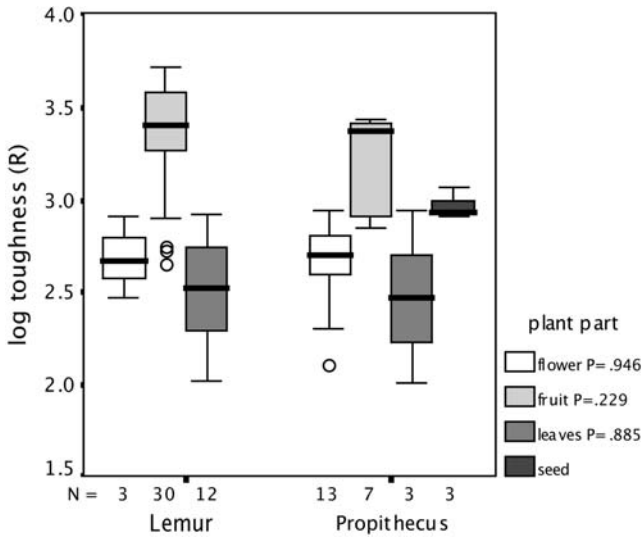
The toughness of kily parts eaten by ringtailed lemurs was significantly higher than that eaten by sifakas (Mann-Whitney  $U$ ,  $Z = -2.148$ ,  $P = 0.032$ ,  $n = 45$  for ringtailed lemurs and 26 for sifakas; Fig. 17.5). However, in comparisons of individual plant parts, there were no significant differences between the two species (Mann-Whitney  $U$ ; see Fig. 17.6, Table 17.2 for comparisons of specific plant parts).



**Fig. 17.4** Logged toughness ( $R$ ) values of phenophases of *Tamarindus indica*. NL, new leaves; YL, young leaves; ML, mature leaves; SD, unripe fruit seed; unrp FR, unripe fruit; rp FR, ripe fruit; FL, flower. Error bars represent one standard error of the mean. Toughnesses of plant parts are significantly different from one another at  $P < 0.0001$  (Kruskal-Wallis on raw values; figure is logged for clarity)



**Fig. 17.5** Toughness ( $R$ ) comparisons of entire *kily* diet of two lemur species. Boxes represent central half of data divided by median line; whiskers are data points that lie from the top of the box to 1.5 times the data range of the box; circles indicate outliers that lie between 1.5 and 3 times the data range of the box; and asterisks are data points that lie beyond 3 times the data range of the box.  $Lc R = 1900.22 \text{ J m}^{-2}$  (SE, 230.82);  $Pvv R = 892.19 \text{ J m}^{-2}$  (SE, 151.24). Comparison is significant ( $P = 0.032$ , Mann-Whitney U on raw values; figure is logged for clarity)



**Fig. 17.6** Toughness ( $R$ ) comparisons of individual *kily* plant parts between the two lemur species. Comparisons of individual plant parts between lemur species are not significant (Table 17.1; non-parametric comparisons on raw values; figure is logged for clarity.). No comparisons of seeds since *L. catta* was not observed eating them. See Fig. 17.5 caption for explanation of symbols

**Table 17.2** Comparisons between lemur species of toughness of *kily* parts eaten<sup>a</sup>

Plant part	$n^b$	$Z$	$P$ -value
Flower	3, 13	-0.067	0.946
Fruit	30, 7	-1.202	0.229
Leaves	12, 3	-0.144	0.885

<sup>a</sup> Mann-Whitney U-test.

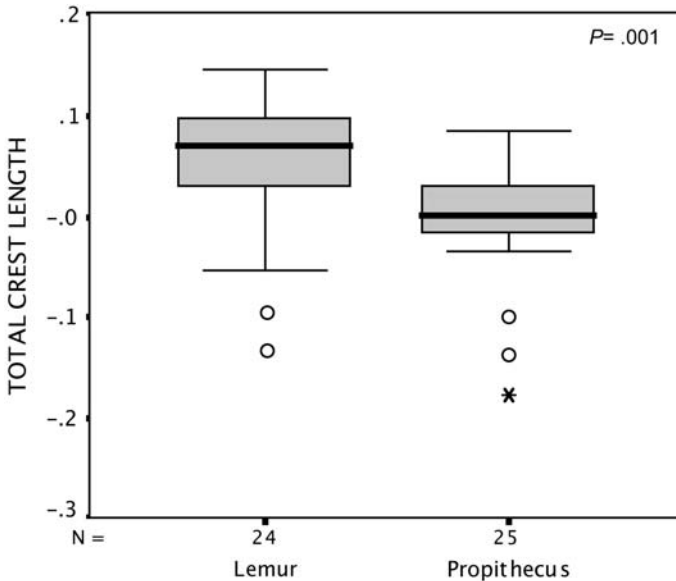
<sup>b</sup> Sample sizes for *L. catta* and *P. verreauxi*, respectively.

Indentation hardness of unripe and ripe fruits and seeds eaten by the lemurs were also compared, and the hardness values of the lemur species were not significantly different from one another (Mann-Whitney U,  $Z = -0.682$ ,  $P = 0.495$ ; *Lc*  $H = 6.75$  MPa,  $SE = 2.16$ ,  $n = 8$ ; *Pvv*  $H = 22.10$  MPa,  $SE = 11.05$ ,  $n = 4$ ). Hardness values are calculated using a model that may change by a constant in future analyses. Relative differences in indentation hardness of foods between species are unaffected.

Ripe *kily* fruit shells were subjected to bending tests, and the two fragmentation criteria,  $\sqrt{ER}$  and  $\sqrt{R/E}$ , were calculated ( $\sqrt{ER}$ : mean = 1459.29,  $SE = 238.45$ ,  $n = 5$ ;  $\sqrt{R/E}$ : mean = 2.161,  $SE = 0.207$ ,  $n = 5$ ). Values for stress-limited defenses were several orders of magnitude higher than those for displacement-limited, suggesting that the ripe fruit shell is quite brittle.

### 17.3.3 Molar Morphometrics

Ringtailed lemurs had relatively longer crests than sifakas when these features were compared using within-family residuals (Mann-Whitney U,  $Z = -3.430$ ,  $P = 0.001$ ; Fig. 17.7, Table 17.3). In addition, the fit of the protocone/talonid occlusal pair was significantly tighter in the ringtailed lemurs (Mann-Whitney U,  $Z = -3.867$ ,  $P < 0.001$ ; Fig. 17.8, Table 17.3). All other comparisons were not statistically significant (Figs. 17.9, 17.10, Table 17.3).



**Fig. 17.7** Comparisons of total crest lengths between ringtailed lemurs and sifakas using within-family residuals. Comparison is significant ( $P = 0.001$ ). See Fig. 17.5 caption for explanation of symbols

**Table 17.3** Comparisons of tooth features between the two lemur species<sup>a</sup>

Tooth feature	$n^b$	$Z$	$P$ -value
Talonid	24, 26	-0.272	0.786
Total crest length <sup>c</sup>	24, 25	-3.430	0.001 <sup>g</sup>
Average cusp radius <sup>d</sup>	17, 21	-1.864	0.062
Average cusp height <sup>e</sup>	24, 26	-0.194	0.846
Protocone/talonid radii <sup>f</sup>	15, 20	-3.867	< 0.001 <sup>h</sup>
Hypoconid/trigon radii <sup>f</sup>	11, 18	-0.584	0.559

<sup>a</sup> Mann-Whitney U-tests on lower molar residuals calculated within families.

<sup>b</sup> Sample sizes for *L. catta* and *P. verreauxi*, respectively.

<sup>c</sup> Sum of all upper and lower molar crests.

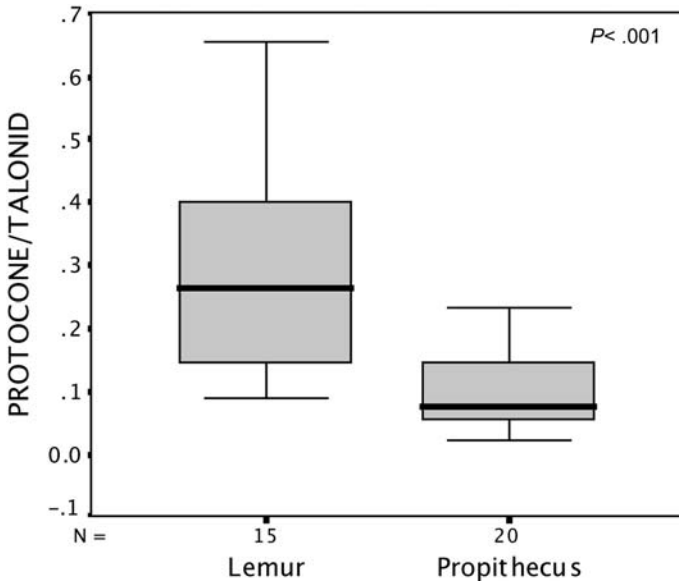
<sup>d</sup> Mean of all upper and lower molar cusp radii.

<sup>e</sup> Mean of all upper and lower molar cusp heights.

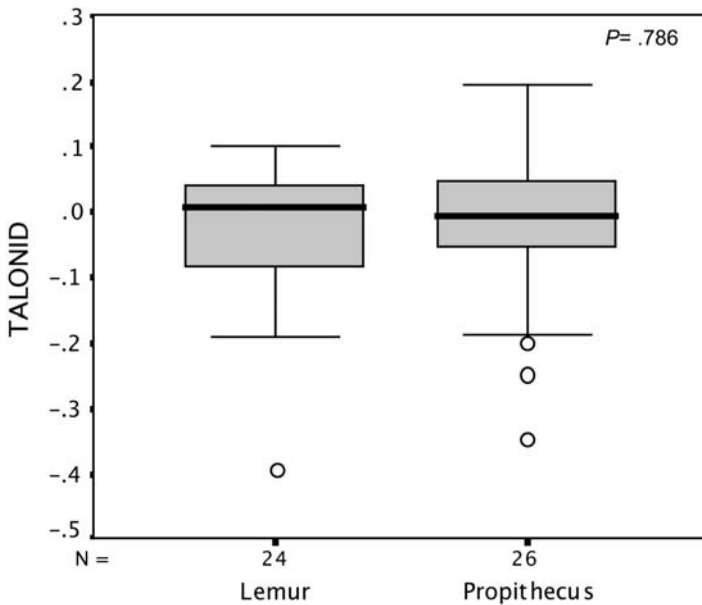
<sup>f</sup> Raw data values used instead of residuals.

<sup>g</sup> Longer crests in *L. catta*.

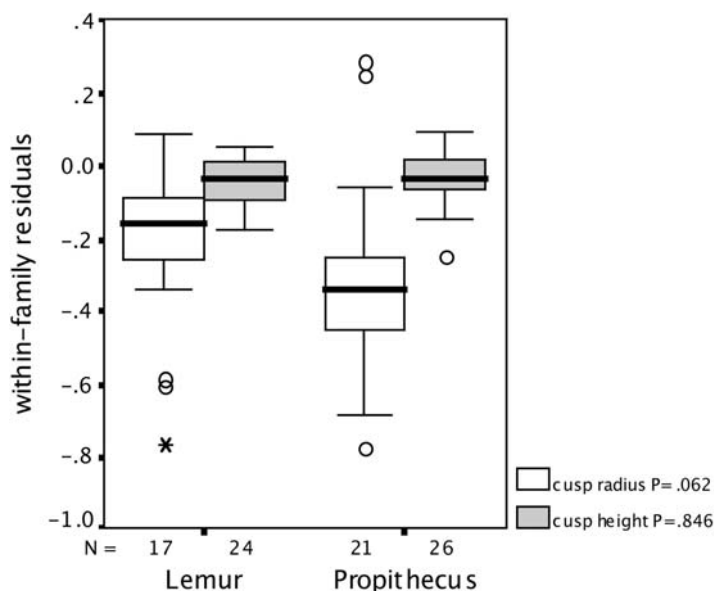
<sup>h</sup> Smaller ratio (looser fit) in *P. verreauxi*.



**Fig. 17.8** Comparisons of protocone/talonid radii between ringtailed lemurs and sifakas using raw data values. Comparison is significant at  $P < 0.001$ . See Fig. 17.5 caption for explanation of symbols



**Fig. 17.9** Comparisons of talonid basin area between ringtailed lemurs and sifakas using within-family residuals. Comparison is not significant ( $P = 0.786$ ). See Fig. 17.5 caption for explanation of symbols



**Fig. 17.10** Average cusp radius and height between ringtailed lemurs and sifakas using within-family residuals. Comparisons are not significant ( $P = 0.062$  and  $0.846$ , respectively). See Fig. 17.5 caption for explanation of symbols

## 17.4 Discussion

### 17.4.1 Comparisons of Tooth Features

The predicted relationships between mechanical food properties and specific tooth features fared equivocally in light of the lack of separation between the lemur species in food toughness and hardness. As predicted, ringtailed lemurs with their relatively longer crests ate tougher foods, though this may be overestimated (see below). Though the species with the blunter cusps did not eat the hardest food (the difference was not significant), the slightly blunter cusps of ringtailed lemurs may help them crack brittle kily fruit shells. Sifakas had a looser occlusal fit of the protocone to the talonid, though it had a less-tough diet than ringtailed lemurs.

However, the high toughness values for the ringtailed lemur diet are largely due to the ripe kily fruit shell. Having a loose occlusal fit, as was predicted for tough foods, would not have helped fragment kily shell since, being a brittle, stress-limited material, it must be cracked not cut (Fig. 17.2). Most of the toughness differences between the lemur species are attributable to their selection of kily fruits at different developmental stages. The force–displacement graph in Fig. 17.2 illustrates the differences in toughness between unripe and ripe fruit stages. Though the ripe kily shell is tougher, the dropoffs from the multiple peaks show where side cracks and runaway cracks appear. Because the scissors were controlling the crack direction,

runaway propagation was limited, and as a result, in all likelihood, the test overestimated the actual toughness of the shell. When ringtailed lemurs break open kily fruit, they do not guide the formation of the crack. They instead apply multiple bites with their canines and premolars to start a crack (Sauther et al., 2001), then tear off the parts that break. In contrast, opening an unripe fruit requires the application of constant stress to initiate and continue crack formation, since runaway propagation does not occur. Unripe fruit ( $R = 1199 \text{ J m}^{-2}$ ) may not be as tough externally as ripe fruit ( $R = 3112 \text{ J m}^{-2}$ ), though again this may be overestimated, but the pulp and exocarp has to be continuously worked. The exterior of unripe kily fruit is also quite hard (8.964 MPa, unripe fruit; 4.568 MPa, ripe fruit). In contrast to unripe fruit, once the brittle casing of ripe fruit has been cracked, the jelly-like pulp is licked off. Unripe fruit (and leaf material) may impose cyclical loads on the masticatory apparatus that is countered by the greater robusticity of the sifaka mandible. Ringtailed lemurs exploit unripe fruit pulp when no ripe fruit is available. The combined effects of exploiting ripe and unripe kily fruits may contribute to the greater postcanine tooth loss and wear seen in ringtailed lemurs compared to sifakas (Cuozzo and Sauther, 2006).

Furthermore, Yamashita (1998a) showed that a loose occlusal fit of cusp to basin was related to eating large quantities of leaf material and not necessarily to food toughness. Crest length was another feature that was correlated with flat leaf geometry. Although sifakas ate less kily leaf material than ringtailed lemurs (Fig. 17.3), young and mature leaves form the bulk of their larger diet (Yamashita, 2002; in prep.).

Perhaps somewhat surprisingly, some tooth features, such as crest length, are relatively greater in size in ringtailed lemurs. In fact, Yamashita (1998b) found that *Lemur catta* and *Indri indri* had the longest crests within their respective families (Table 17.1). Of course, the results presented here are predicated on the *relative* differences within families being the functionally significant comparison. If tooth features are compared to lower molar area without regard to family (Yamashita, 1998b), then sifakas have larger and longer features than ringtailed lemurs, with the sole exception of the ratio of the protocone to the talonid. Food size, especially of a shared resource such as kily, would presumably be invariant, which supports the idea that “absolute” size of tooth features is more critical. However, analyses of covariance between the lemurids and the indriids demonstrated that slope differences were not and intercept differences were significantly different for the tooth features examined here. Taxonomic affiliation constrains tooth features along parallel slopes between families. While larger and longer features may be preferable, the species have inherited morphologies imposed by their respective families. That indriid features are generally larger at the same tooth size speaks to the homogeneity and potential stabilizing selection on these features within the Indriidae. The relative elongation of crests in ringtailed lemurs is indicative of an adaptive shift within the family. Ringtailed lemurs are in a sense approaching the sifaka condition. The reasons for this are purely speculative, but may be related to commonalities of diet. Yamashita (1996) found that the diets of ringtailed lemurs, in terms of hardness, shear strength, and food type, had more in common with sympatric sifakas than with their rainforest confamilials, *Eulemur fulvus rufus*, and *Eulemur rubriventer*.

### 17.4.2 Comparisons with Larger Diet

Kily food parts are not necessarily representative of the larger diet in terms of the actual time spent on specific parts or their mechanical properties. One of the cautionary tales learned here is that one has to be careful about extrapolating to the larger diet even from a prominent, though highly seasonal, component. Somewhat contrary to their expected dietary classifications, the ringtailed lemurs focused on kily fruit pulp and young leaves and sifakas spent the most time on flowers. This deviates somewhat from the larger diet, in which ringtailed lemurs spend equal amounts of time on fruits and leaf material (31% and 38%, respectively), while sifakas overwhelmingly spend the majority of feeding time on leaf material (12% on fruits and 64% on leaves; Yamashita, 2002). The differences found between the whole diet and the kily subset is most likely related to the relative importance of kily to the two lemurs. Kily food parts, and especially ripe fruits, are major components of the ringtailed lemur diet (29% of total time spent feeding), and, while important, they are less prevalent in the diet of sifakas (11%).

Earlier work found that the two species' diets did not differ significantly in hardness and toughness, though sifaka diets had higher seed hardness thresholds (Yamashita, 2000, 2002). Up to around 12 MPa, seeds were masticated so that nothing identifiable appeared in the feces. Above this level, the seed was discarded, as ripe kily seeds were. Ring-tailed lemurs had a lower threshold at 4 MPa. Seeds generally passed through the digestive tract intact and were defecated, and the defecated seeds were not as hard as those rejected by sifakas.

In the current study, the toughness of the overall kily diet was significantly higher in ringtailed lemurs than in sifakas. As discussed above, this is most likely due to the toughness of kily fruit shells. Kily plant parts represent extremes on toughness and hardness scales with respect to the larger diet for both lemur species. Comparing the kily diet to the entire diet, average  $R$  was  $1900.22 \text{ J m}^{-2}$  and  $810.87 \text{ J m}^{-2}$ , respectively, for ringtailed lemurs, and  $892.19 \text{ J m}^{-2}$  and  $585.63 \text{ J m}^{-2}$  for sifakas. Hardness values also represented extremes in the kily diet: 6.75 MPa (kily parts) and 4.91 MPa (whole diet) for ringtailed lemurs and 22.10 MPa and 12.65 MPa for sifakas, respectively.

Because kily plant parts lie at the mechanical extremes of the diets of the two lemur species, they may represent fallback foods, eaten when preferred foods are not available (Wrangham et al., 1998; Furuichi et al., 2001; Lambert et al., 2004). However, ripe kily fruit, though the toughest food eaten, is an important component of the ringtailed lemur diet throughout the year (Sauter, 1998; Yamashita, 2002). Seeds eaten from unripe kily fruit by sifakas may represent a fallback food, since they are eaten at restricted times of the year and the unripe fruit exterior is harder than the overall diet. Indriids, however, are seed predators in addition to being folivores (Hemingway, 1996; Yamashita, 1998a; Powzyk and Mowry, 2003), so interpreting unripe kily fruit seeds as "fallback foods" may not be strictly accurate.

Kily food parts appear to have a greater significance to ringtailed lemurs in terms of total dietary contribution and the demands they place on the masticatory apparatus. The specific molar features of ringtailed lemurs, though in some cases relatively



larger, are absolutely smaller than in sifakas, which makes breaking down foods with similar mechanical properties a comparatively greater challenge. Cuozzo and Sauter (2004) report the most severe tooth wear and loss on the P3-M1, where ripe kily fruit pods are often initially inserted. Ripe kily fruit has a high sugar content that proves irresistible to these lemurs despite the mechanical challenges (Yamashita, 2008). Since ringtailed lemur molar features are elaborated in the same directions as those of sifakas, kily food parts may be exerting some sort of selection on the ringtailed lemur masticatory apparatus toward a sifaka-like morphology.

Ripe kily fruit relies on stress-limited defenses since the lemur has to exert enough force to crack the shell and initiate crack formation. The shell is quite brittle. For unripe fruit and the seeds contained within, toughness appears to be the primary mechanical defense. This also applies to leaves at different phenophases. The fit of the protocone to the talonid basin in sifakas may also be an indication of displacement-limited defenses in leaf material since the looser fit allows greater excursion of the cusp and crest within the basin for cutting leaves. However, other properties may be more appropriate for offering defenses against predation.

Chemical properties of kily plant parts support their mechanical distinctiveness and offer further insights as to why the two species differ in selection of kily plant parts that are related to metabolic requirements and tolerances for secondary plant compounds (Yamashita, 2008). The ringtailed lemurs' preference for ripe kily fruit is probably related to its high sugar content. Young kily leaves provide the highest amounts of protein to a species that is relatively lacking in other protein sources. In a complementary fashion, sifakas take in more protein and less sugar. The seeds and flowers eaten by sifakas are high in protein, and mature kily leaves contain higher amounts of sugar than earlier phenophases. At the same time, the ripe fruit largely consumed by ringtailed lemurs contains relatively low amounts of secondary plant compounds. Sifakas take in much higher levels in combination in mature leaves, seeds, and flowers.

## 17.5 Conclusions

The "curious" nature of kily lies in how thoroughly the two sympatric lemur species exploit its edible parts while minimizing overlap on them. Though there is some small degree of overlap in some of the plant parts, actual feeding times reveal biases for key parts that are only partially related to their mechanical properties. The distinctive preferences for specific kily parts mirror chemical preferences and aversions in their larger diet.

The expected relationships between molar features and mechanical properties were generally upheld. Ringtailed lemurs had relatively longer crests and ate tougher kily parts than sifakas, though the toughness of the primary diet (ripe kily fruit) may have been overestimated. Though food hardness was not significantly different between the lemur species, the slightly blunter cusps of ringtailed lemurs may help them crack brittle kily fruit shells. The looser protocone/talonid occlusal fit in sifakas is probably related to reducing tough leaf material with a uniform geometry.

As important as kily is to the diets of both species, it is not representative in terms of the mechanical properties of its parts. Kily food parts lie at the extremes of toughness and hardness ranges representing the entire diets of both lemur species. Though the individual parts are mechanically distinctive, the kily diets of the two lemurs did not segregate mechanically, except for ripe kily fruit shells that were tougher than other foods.

Since kily plant parts represent the mechanical extremes of the overall diets for both species, they could potentially help clarify the debate concerning the relative importance of the properties of the most frequently eaten or the most stressful foods on morphology. The data presented here and from other fieldwork on mechanical food properties, however, have shown that the debate cannot readily be resolved. In the present case, the geometry of the most frequently eaten food, leaf material, relates to the unconstricted basins of sifakas, whereas the extreme toughness of kily fruit shell is related to the long crests in ringtailed lemurs.

Kily parts form a greater proportion of the total diet for ringtailed lemurs, and, because these parts represent mechanical extremes compared to the rest of the diet, it is probably more stressful for ringtailed lemurs than sifakas when eating them. Interestingly, ringtailed lemurs have relatively larger molar features than sifakas (though sifaka features are “absolutely” larger), which indicates that they are approaching a sifaka-like morphology for fracturing similar diets.

The integration of fieldwork with morphology yields insights into how animals use their particular morphologies and, conversely, how morphologies constrain and/or direct behavior and food choice. In the case of the two lemurs investigated here, food properties appear to be directing morphology in the ringtailed lemurs, while, in sifakas, their morphology constrains them to foods within a range of properties.

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