Food Procurement and Tooth Use in Two Sympatric Lemur Species

Nayuta Yamashita*

Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, California 90089-9112

KEY WORDS diet; ingestion; mechanical food properties; toughness

ABSTRACT This study of two lemur species (*Lemur catta* and *Propithecus v. verreauxi*) in Madagascar combines observations of food procurement and initial food placement in the mouth with comparisons to food toughness and external properties. Food toughness was hypothesized to play a decisive role in determining food placement during ingestion. It was found that tougher foods are generally ingested on the postcanines for all foods eaten. However, when leaves and fruits are analyzed separately, food size and shape, represented here by mass and food type, are more reliable predictors of initial food placement. Larger leaves and bulkier fruits and stalks are ingested posteriorly. Leaf toughness is not related to leaf size, though the toughness and size of the most commonly eaten fruits are correlated. Furthermore, ingestive food toughness, which is the maximum toughness, and "average" food toughness may make different mechanical demands on the masticatory apparatus that have consequences for jaw morphology. Am J Phys Anthropol 121: 125–133, 2003. © 2003 Wiley-Liss, Inc.

During the ingestive phase of feeding, food is brought to the mouth in preparation for further oral processing. Few studies specifically focus on modes of ingestion (but see Izawa and Mizuno, 1977; Milton, 1978; Iwano and Iwakawa, 1988; Ungar, 1994); observations on food intake are often reported within the context of general feeding behaviors. From these studies, it appears that foods are prepared at different positions on the toothrow. Whole fruits are frequently taken in anteriorly, where incisors and canines expose the fruit flesh (Ungar, 1994). Seed predators extract seeds following anterior preparation and process them on the cheek teeth (Kiltie, 1982; Happel, 1988; Iwano and Iwakawa, 1988; Kinzey and Norconk, 1990; Lucas et al., 1994). Exudate feeders gouge bark with their lower anterior teeth, to liberate gum and nectar (Kinzey et al., 1975; Coimbra-Filho and Mittermeier, 1976; Nash, 1986). Manipulation of foods can also precede or accompany insertion into the mouth. Bamboo shoots, for example, are husked by guiding them into the side of the mouth and pulling them through the opposite side (Milton, 1978; Santini-Palka, 1994). Insect ingestion has been observed as a two-part, "gape-shove" sequence that first involves grabbing the prey with the hands, followed by biting it on the anterior teeth and postcanines (Jablonski and Crompton, 1994). In some extreme cases, seeds and nuts are first pounded against a substrate prior to ingestion (Izawa and Mizuno, 1977; Peres, 1991; Marchant and McGrew, 2002).

A combination of properties apparently influences where food items are initially placed in the mouth. Resistant seeds are placed posteriorly to take advantage of the greater bite forces generated closer to the mandibular condyle (Kiltie, 1982), while long stalks and stems require insertion into the side of the mouth for efficient processing. Such references to food texture and geometry describe physical properties of foods, which can be further classified into external and internal categories (Lucas et al., 1986). External properties include food geometry (e.g., size and shape) as well as its surface texture (e.g., roughness, stickiness). Internal or mechanical properties (e.g., strength, toughness, stiffness) are usually discussed in engineering terms and describe the material composition of the food, which contributes to the ability of the structure to resist fragmentation (for a thorough review, see Strait, 1997). The present study examines the relative importance of external vs. internal properties on initial food placement.

Mouth-size pieces of food are bitten off during ingestion and are then finely fragmented during the

Grant sponsor: Research Grants Council of Hong Kong; Grant sponsor: National Geographic Society.

*Correspondence to: Nayuta Yamashita, Department of Cell and Neurobiology, Keck School of Medicine, BMT 408, University of Southern California, 1333 San Pablo St., Los Angeles, CA 90089-9112. E-mail: nayutaya@usc.edu

Received 6 December 2001; accepted 25 September 2002.

DOI 10.1002/ajpa.10206

chewing phase. Decisions on the suitability of a potential food based on its mechanical properties will first be made when the food is ingested (Dominy et al., 2001). The primate consumer must decide whether it can overcome the mechanical defenses of the plant part and where to process it at this point. Stated from a slightly different perspective, ingestion is the beginning of a process wherein a herbivore first breaks apart foods and the plant defends itself from being fragmented. (Ripe fruits are an obvious exception since they are intended to attract dispersers for their seeds, although key dispersers may be targeted to the exclusion of others.)

Food fragmentation depends on crack formation (Gordon, 1976). The internal composition of a plant part determines how it resists the formation of cracks that can ultimately break it apart. Empirical work has established that the relationship between two mechanical properties, toughness (R) and elastic modulus (E), describes how foods fragment (Agrawal et al., 1998; Lucas et al., 2001). Toughness is the work required to fracture food. Tough foods resist crack formation, are good at stopping cracks once they start, and are often able to undergo large deformations before they fail. Elastic modulus is a measure of stiffness, or stress divided by strain on a force-displacement graph.

Plants use toughness and stiffness as defenses against herbivory (Lucas et al., 2000). Displacement-limited defenses rely on the herbivore not being able to sufficiently strain the plant part to failure in order to fragment it. Stress-limited defenses depend on the herbivore being unable to generate sufficient force to break open the plant part. Stress-limited foods tend to be brittle and shatter when sufficient stress levels are reached. The product of elastic modulus and toughness (E*R) has been shown to describe stress-limited defenses, and displacement-limited defenses are described by toughness divided by elastic modulus (R/E) (Agrawal et al., 1998). Thin sheets of material, such as leaves, tend to rely solely on toughness as a defense.

Ingestion can occur anywhere on the toothrow (as the field studies above showed), whereas mastication occurs solely on the postcanines. Tough foods, which are displacement-limited, are finely fragmented on the specialized morphology of the postcanines. Food toughness, therefore, may have a greater impact during mastication than during ingestion (P. Lucas, personal communication). More resistant foods, whether stress- or displacement-limited, however, will likely be ingested on the postcanines. The greater muscle force generation that occurs posteriorly induces crack formation in hard, stress-limited foods. Since displacement-limited defenses are overcome on the postcanines during mastication, the same morphology that breaks down tough foods (crests, occluding cusps, and basins) may also be used for biting off mouth-sized pieces. Placing foods in the mouth where they have the highest probability of being fractured should also increase the efficiency of feeding.

While mechanical food properties play an important role in feeding decisions by primates (Yamashita, 1996, 1998), little is known about how physical properties as a whole contribute to the beginning of the process. This paper is an initial foray into examining the degree to which physical food properties (including food toughness, size, and shape) affect where foods are ingested on the toothrow. Toughness is the only mechanical property examined because of the preponderance of leaves in the diets of the two lemur species studied (Yamashita, 2002). Given that tough foods are processed posteriorly (e.g., Hiiemae and Crompton, 1985; Janis and Fortelius, 1988; Lucas and Teaford, 1994), the expectation is that these same foods will be initially ingested at the same location, with the added benefit of expediting feeding. Less tough foods are expected to be ingested more anteriorly. Furthermore, observations from many studies (see above) show that external physical properties such as food size and shape are involved in feeding decisions during ingestion. These variables are also included in the analysis.

Finally, plant parts were tested at several locations on the plant. The position on the plant where food is initially harvested may be the most mechanically challenging part that the animal handles, since the plant will defend itself mechanically to discourage first bites. Therefore, the toughness of the foods where they are initially bitten off probably represents a maximum toughness value for that food item. The average toughness of a food, however, may be a better indicator of the loads that the masticatory apparatus bears during mastication. The point where foods were bitten off and more distal locations on the same plant part were tested as "ingestive" toughness and "average" toughness, respectively.

In summary, this paper describes 1) distinguishing characteristics of foods that are placed in the front or side of the mouth, 2) how the toughness and geometry of these foods are related to their placement during ingestion, and 3) differences between ingestive and average toughnesses of foods. The working hypothesis is that toughness alone determines where foods are placed on the toothrow during ingestion, and that tougher foods will be ingested on the postcanines.

MATERIALS AND METHODS

Observations

Six sifaka (*Propithecus v. verreauxi*) and five ring-tailed lemur (*Lemur catta*) groups were studied intensively in an 11-month study during February 1999–February 2000 at the Beza Mahafaly Special Reserve in the dry forest of southwestern Madagascar. The animals were followed with focal animal observations that were facilitated by identifying collars and pendants on individuals within each group studied. Focal animals were switched every 10 min. Observations during continuous bout sampling focused on ingestive and feeding behaviors. Observation conditions were excellent; it was possible to approach to within a few meters of habituated animals.

During focal observations, food plants were flagged for later collection and were usually collected within a few hours of observation. Foods dropped by the animals were obtained whenever possible. The plant species tested, plant parts tested, sample sizes, and locations on the plant where toughness tests were conducted are listed in the Appendix.

In most cases, the foods were bitten off and not plucked manually. The two lemur species used either the anterior teeth (incisors) or the postcanines to bite off whole fruits, leaves, flowers, and stalks. Tooth use was classified into several categories during observations, following Ungar (1994):

Incisor: foods are placed anteriorly in the mouth during ingestion.

Nip: food is placed directly in the front of the mouth and bitten off. This category also includes holding the food with the tongue and pulling the head back.

Strip: food is placed in the front of the mouth and pulled out anteriorly. Foods treated in this manner are bipinnate leaves, vines, and stalks, which are not limited to this mode of ingestion.

Scrape: incisors (tooth comb) are used to scoop or gnaw food.

Postcanine: foods are inserted into the side of the mouth.

Nip: food, usually leaves and flowers, is placed directly on the postcanines and bitten off.

Strip: food is inserted into the side of the mouth and pulled out through the side.

Crush: food, usually fruit, is placed directly on the postcanines and bitten through.

Chew: most foods are finely masticated on the postcanines.

Plant testing and statistical analyses

Special attention was paid to the specific point where foods were bitten off, and the toughness (in J/m^2) of these positions was tested with a portable mechanical tester (Darvell et al., 1996; Lucas et al., 2000).

Sample sizes and specific locations on the plants where they were tested are listed in the Appendix. The numbers of times plants were tested are consistent with the numbers of observations of lemurs eating a specific plant part. The most frequently tested foods in the Appendix were the most frequently eaten foods. Three to four individual plant parts were tested for each plant species every time the species was tested.

Ingestive and average toughnesses were tested for most plant parts. Leaves were tested either at the petiole or at the base including the midrib, where they were most commonly bitten off. "Average" toughness for a leaf is defined as a cut through the midpoint of the leaf that includes the midrib (Lucas et al., 1998). Bipinnate leaves were tested either on the rachis or pinnae that support individual leaflets for ingestive toughness, and through the pinnules for "average" toughness. Flowers were most often tested at the individual pedicel that supports the flower, and either the average toughness of individual flower parts (petals, sepals) or the toughness through the nectary was taken to represent the "average" value. Fruits were tested according to the first part encountered, in most cases the fruit shell or fleshy mesocarp with attached exocarp. The stems of small fruits were tested separately from the fruit flesh when they were ingested in one bite. Stems and stalks that were dropped by the animals or collected with bite marks on them were tested just proximal to where they were bitten. Stalks that were collected adjacent to where animals were feeding were tested at the approximate position of the original bite marks.

Finally, food variables were analyzed statistically. The dataset was constructed with four variables: ingestive location on the toothrow (1, anterior; 2, postcanine; and 3, combination), food type (leaf, fruit, flower, stalk, or shoot), food toughness at the bite point, and food mass. Food type was used as a proxy for shape, because at this level of analysis the geometry of a food item was adequately described by its gross category. As an example, fruits as a category have an overall similarity in dimensions that separate them from leaves, stalks, and flowers. Food mass provided information on differences in food size within the categories used. All variables were compared with nonparametric statistics on untransformed data.

RESULTS

Distribution of variables along tooth row

Tougher, heavier foods are ingested on the postcanines instead of the incisors (Mann-Whitney U $P = 0.000$ for both toughness and mass; Fig. 1). Ingestion of a greater variety of plant parts also occurred on the postcanines, since stalks were usually inserted in the side of the mouth (Appendix). Only fruits and leaves, and occasionally flowers, were consistently ingested in both locations (Appendix).

To clarify the relative importance of food toughness and size (mass) to initial placement and to minimize the effects of food shape, leaves and fruits were analyzed separately. Both food types are ingested in both areas of the tooth row, and they exhibit variation in toughness and size. Though toughness of all foods is generally higher on the

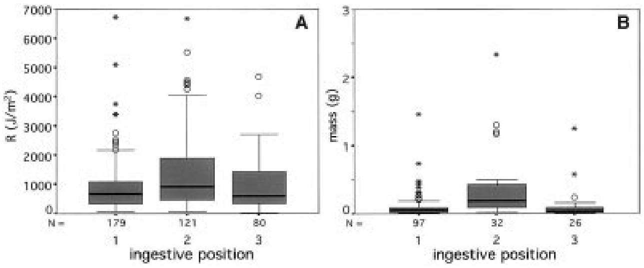

Fig. 1. Toughness (**A**) and mass (**B**) of all foods eaten with respect to where they were initially ingested on the tooth row. Boxplots reveal positive skew of data. Mann-Whitney U $P = 0.000$ between positions 1 and 2 for both A and B. 1, anterior; 2, postcanine; 3, combination. Boxes represent central half of data, line inside represents median, and whiskers are data points that lie from top of box to 1.5 times the data range of box. Circles indicate outliers that lie between 1.5–3 times the data range of box, and asterisks are data points that lie beyond 3 times the data range of box. All data are untransformed. Means and standard deviations for each position are as follows. A: 1 = 886.06 (860.02); 2 = 1,450.95 (1,330.14); 3 = 970.98 (931.18). B: 1 = 0.10 (0.19); 2 = 1.37 (4.06); 3 = 0.12 (0.26). Large standard deviations occur as a result of grouping numerous plant parts and plant species within each ingestive position.

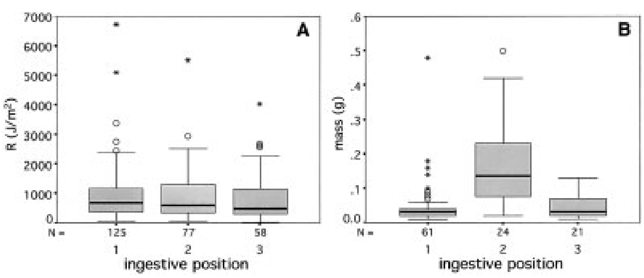

Fig. 2. Toughness (**A**) and mass (**B**) of leaves eaten with respect to where they were initially ingested on tooth row. A: Mann-Whitney U $P = 0.728$. B: Mann-Whitney U $P = 0.000$ between positions 1 and 2. Conventions follow Figure 1. Means and standard deviations for each position are as follows. A: 1 = 913.59 (900.32); 2 = 915.81 (815.78); 3 = 828.79 (819.31). B: 1 = 0.005 (0.007); 2 = 0.18 (0.13); 3 = 0.005 (0.004).

postcanines (see above), leaves showed no differences in ingestive toughness in either position in the mouth (Mann-Whitney U $P = 0.728$; Fig. 2A). Heavier leaves were ingested on the postcanines (Mann-Whitney U $P = 0.000$), and there was no significant correlation between toughness and mass (Spearman's rho = -0.154; $P = 0.059$; Fig. 2B), further reinforcing the finding that toughness is not related to initial food placement for leaves. Whatever relationship toughness has with food placement during ingestion (as found in Fig. 1), then, must be related to its correlation with foods other than leaves. A separate analysis of fruits, which are also ingested in both locations on the toothrow, showed a clear relationship between toughness and mass (Spearman's rho = 0.401; $P = 0.014$) and toughness and placement of fruits (Mann-Whitney U $P = 0.000$; Fig. 3). Both tougher and heavier fruits were ingested on the postcanines.

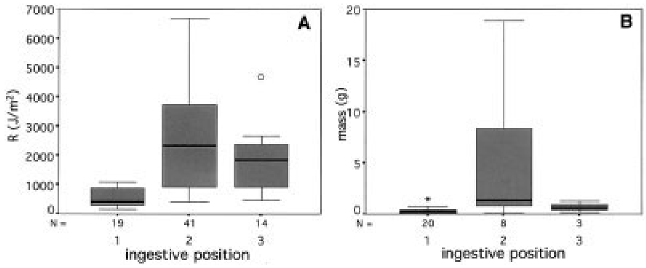

Fig. 3. Toughness (**A**) and mass (**B**) of fruits and stalks eaten with respect to where they were initially ingested on tooth row. Mann-Whitney U $P = 0.000$ between positions 1 and 2 for both A and B. Conventions follow Figure 1. Means and standard deviations for each position are as follows. A: 1 = 559.03 (311.19); 2 = 3,432.70 (1,540.16); 3 = 1,807.79 (1,113.20). B: 1 = 0.31 (0.32); 2= 4.97 (7.30); 3 = 0.67 (0.56).

TABLE 1. Ingestive and "average" toughness values of foods in two positions on toothrow[1]

	Anterior	Posterior
Maximum ingestion	6,725.35 J/m^2	6,695.65 J/m^2
Median ingestion	650.0	900.0
Maximum "average"	1,960.03	4,283.48
Median "average"	350.0	450.0

[1] Median values rather than means are preferred for this comparison because of the positive skew of the data as shown in boxplots. Median values are better indicators of where the majority of data reside.

Comparison of ingestive toughness to "average" toughness

The maximum loads sustained by the different parts of the tooth row during the ingestive phase of feeding are given in Table 1. The maximum toughness of foods ingested anteriorly is 6,725.35 J/m^2 (small leaves eaten by sifakas); on the postcanines, the maximum is comparable at 6,695.65 J/m^2 (stalk eaten by sifakas). The median values for ingestive toughness, however, are much lower, at 650 and 900 J/m^2 for anterior and posterior locations, respectively.

Ingestive toughness is higher than the "average" toughness of all foods eaten (Mann-Whitney U = 0.000; Fig. 4A, Table 1). There are significant differences between the toughness values of ingested leaves and their average values (Mann-Whitney U $P = 0.000$; Fig. 4B), which is also true for fruits (Mann-Whitney U $P = 0.002$; Fig. 4C). However, this latter result, though significant, is an underestimate, since it was not possible in many cases to separate ingestive from average toughnesses for fruits.

Comparison of lemur species

The two species do not demonstrate significant differences in ingestive toughness of leaves (Mann-Whitney U $P = 0.404$). However, when ingestion is divided by location, ring-tailed lemurs and sifakas have opposite patterns of ingestion with respect to food toughness (Fig. 5). Sifakas ingest tougher

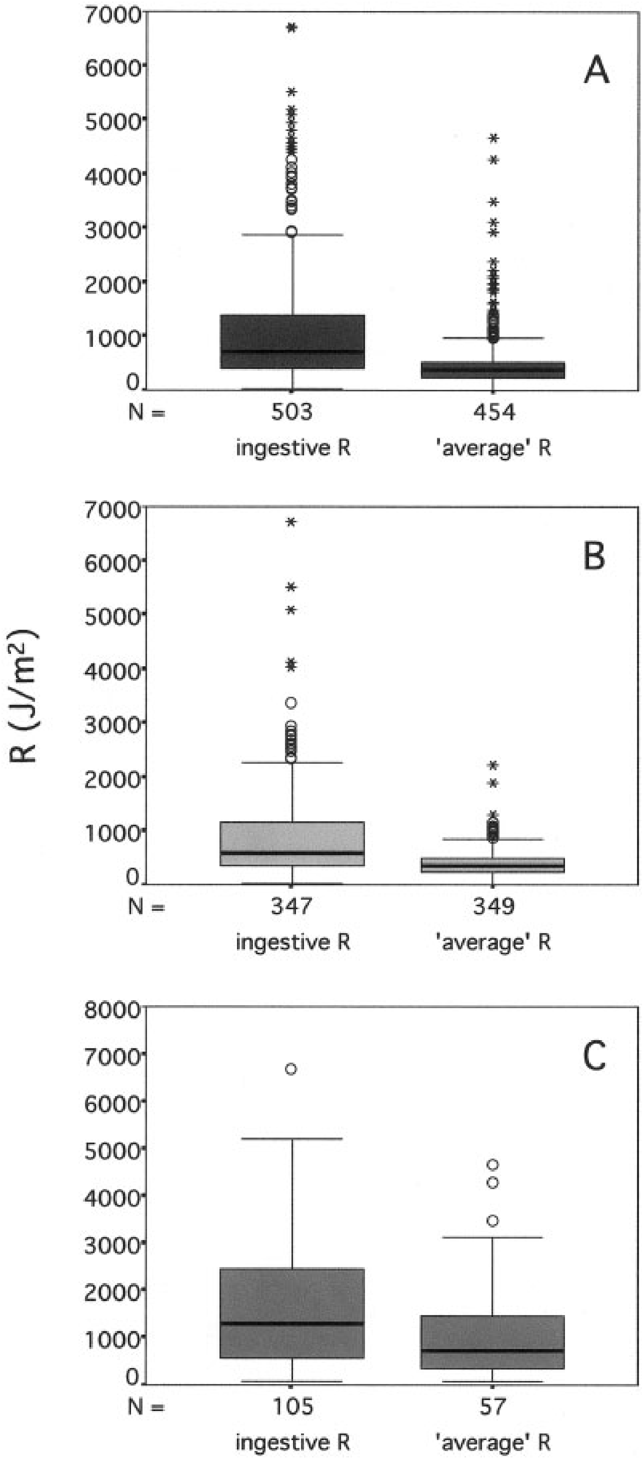

Fig. 4. Comparisons of ingestive toughness to "average" toughness (see text for explanation) for all foods eaten (**A**), leaves (**B**), and fruits (**C**). Mann-Whitney U P = 0.000 for A and B, P = 0.002 for C. Conventions follow Figure 1. Means and standard deviations for each position are as follows. A: Ingestive R = 1,061.30 (1,053.68), "average" R = 481.55 (499.60). B: Ingestive R = 865.86 (815.23), "average" R = 395.72 (260.27). C: Ingestive R= 1,732.90 (1,425.55), "average" R= 1081.19 (1,043.95).

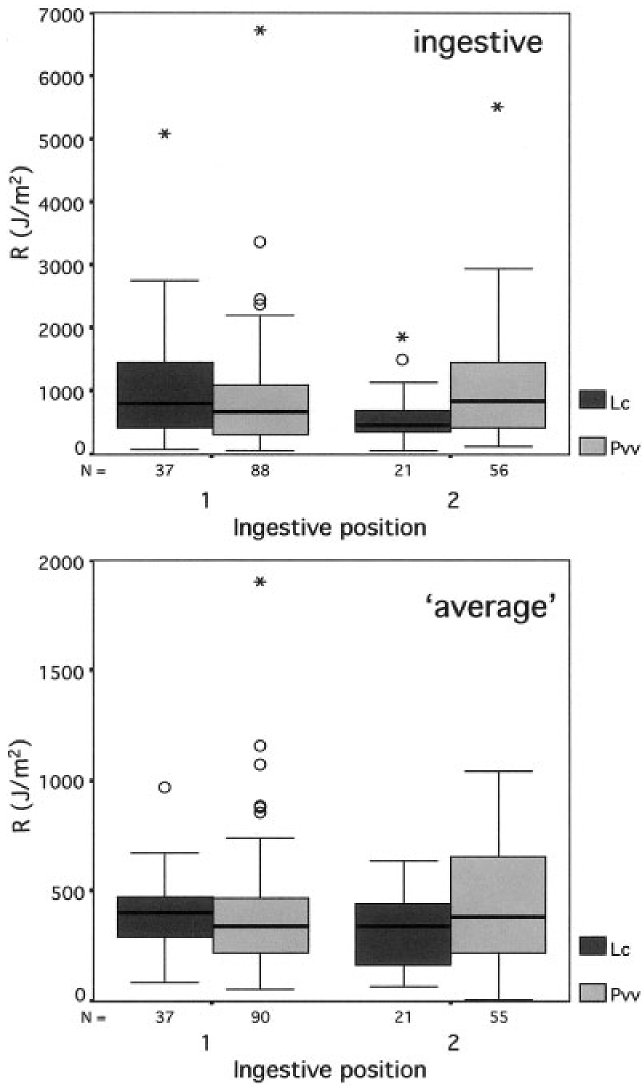

Fig. 5. Toughness comparisons between two lemur species for ingestive (**top**) and "average" (**bottom**) leaf toughness. Top: Position 1, Mann-Whitney U P = 0.446; position 2, Mann-Whitney U P = 0.035. Bottom: Position 1, Mann-Whitney U P = 0.326; position 2, Mann-Whitney U P = 0.096. Lc, *lemur catta*; Pvv, *Propitheans v. verreauxi*.Conventions follow Figure 1. Means and standard deviations for each position are as follows: Top: Position 1, Lc = 1,014.15 (952.36), Pvv = 871.31 (879.71); position 2, Lc = 600.43 (449.40), Pvv = 1,034.08 (891.03). Bottom: Position 1, Lc = 392.82 (177.70), Pvv = 393.85 (269.50); position 2, Lc = 317.81 (163.37), Pvv = 441.48 (263.55).

leaves posteriorly than ring-tailed lemurs (Mann-Whitney U P = 0.035), though anterior leaf toughness is not significantly different between lemurs (Mann-Whitney U P = 0.446). Results are not significant in either ingestive location for average leaf toughness (Fig. 5). Both species overwhelmingly ingest heavier leaves posteriorly (Fig. 2B).

Both species treat fruits/stalks in the same manner. Tougher and heavier fruits and stalks are ingested posteriorly, as shown in Figure 3.

DISCUSSION

Counter to prediction, food toughness is not as important a discriminator of initial food placement as other variables such as size and shape. Food mass reliably separates foods by ingestive position, with heavier foods of all categories ingested on the postcanines. This is not always the case with food toughness. Toughness does not determine where leaves are ingested (their size does), and fruits and stalks that are both tougher *and* heavier are ingested on the postcanines. The general finding of higher toughness for all foods ingested on the postcanines (Fig. 1) tracks fruit and stalk ingestion (Fig. 3). Bulky foods such as fruits and stalks that are ingested on the postcanines are generally tougher than the small leaves, fruits, and flowers that are taken in anteriorly (Figs. 2, 3). An explanation for this pattern is that food geometry is inseparable from its material properties. For stalks, the arrangement and proliferation of structural carbohydrates (cellulose, lignin) on the outer segments of the cylinder confer toughness and rigidity (Niklas, 1992). The majority of large fruits eaten by the lemurs are bulky pods of *Tamarindus indica* (see below) that require high stresses to initiate crack formation on the outer casing (they are stress-limited). Lemurs respond by placing these foods on postcanines, where muscle force generation is greatest. This behavior extends to leaf material insofar as larger leaves are also ingested posteriorly, but, unlike the finding for fruits, leaf toughness is independent of size. Toughness of leaves is conferred by the distribution of veins and the structural elements that surround them (Lucas et al., 1991). The bulk of leaf material, the lamina, contributes little to structural integrity and overall toughness (Lucas et al., 1991). Ingesting large leaves on the postcanines has less to do with generating high stresses to start cracks than with placing them on surfaces with the appropriate morphology for cutting through the veins and reducing particle size.

Toughness and ingestion

Toughness itself may not be the major criterion for initial food breakage during ingestion. Stress limitations may be more important, for which the product of elastic modulus and toughness is the appropriate mechanical index (Lucas et al., 2000). Ordinarily tough foods such as leaves may actually act more stress-limited during the first ingestive bites when they are detached at the petiole or rachis. The results of this study do not contradict this, since initial placement of foods does not appear to be primarily related to food toughness.

It could also be the case that gross breakage of foods during ingestion can be accomplished equally well by either the incisors or postcanines. Food toughness becomes more relevant during mastication, when fine fragmentation of foods must overcome displacement-limited defenses (R/E). Similarly, the mode of ingestion (e.g., nip, strip, crush) initiates fragmentation of foods by overcoming both stress- and displacement-limited plant defenses (P. Lucas, personal communication). These ingestive modes are not confined to a single position on the toothrow, which may partly explain the lack of correlation between ingestion and leaf toughness found here.

Food toughness comparisons between lemur species

Ingestive toughness represents the maximum toughness of foods. High initial leaf toughness is attributable to the greater concentration of structural elements in the midrib near the leaf base where they are bitten off (Lucas et al., 1998). Common fruits eaten require high initial forces to break through the exocarp. In contrast, the average toughness of food items is more indicative of the normal loads the animal experiences while chewing foods. It is the masticatory toughness. The relevance of this distinction is warranted when one considers the greater robusticity of the oral apparatus found in sifakas compared to ring-tailed lemurs (Schwartz and Tattersall, 1985; Ravosa, 1991). Ring-tailed lemurs and sifakas have comparable ingestive toughness ranges for all foods eaten, and ring-tailed lemurs eat more fruits that act very tough (see above). Though fruits act initially tougher than leaves (Fig. 3), once the outer skin or shell is penetrated, the underlying mesocarp offers relatively little resistance to further fragmentation (excluding the seed) (Yamashita, 2002). The outer shell of the most commonly eaten fruit, *Tamarindus indica*, is brittle when ripe, and shatters when sufficient force is applied to it. Leaves, however, must be continuously chewed (displacement-limited). The average toughness of the leaves ingested on the postcanines, though not significantly different between lemur species, is higher for sifakas than for ring-tailed lemurs (Fig. 5). Sifakas are also obligate folivores, whereas ring-tailed lemurs are generalist herbivores that incorporate more fruit and relatively less leaf material in their diet. Fine comminution of tough material, and not simple ingestion, probably underlies sifaka jaw robusticity. There is some circumstantial evidence for this: sifaka feces contain little in the way of identifiable parts, whereas the feces of ring-tailed lemurs contain numerous unchewed particles (personal observations). Though ingestive leaf toughness is higher than masticatory toughness (Table 1), the latter imposes cyclical loads during fine fragmentation that may be related to greater mandibular robusticity to counter bone fatigue (Hylander, 1979).

Finally, the more complex incisive behaviors described by Hylander (1975) and Ungar (1994) in anthropoids were not observed in lemurs. The mandibular anterior teeth in lemurs are elaborated into a tooth comb, which may limit their use as ingestive tools, and fruits with peels that require incisal preparation are largely absent from the site.

CONCLUSIONS

Food toughness does not play a central role in food placement during ingestion. Initial ingestive position appears to be related to the size of the food. Small leaves, flowers, and fruits are ingested anteriorly, whereas heavier, bulkier foods (large leaves, flowers, and fruits and stalks) are ingested on the postcanines. Toughness, at least considered singly, does not appear to be directly related to food placement. The initial finding of a relationship between food toughness and ingestive position results from a positive correlation between fruit mass and toughness on the postcanines. The heaviest fruits most commonly eaten by these lemurs are stress-limited and initially act quite tough.

A distinction can be made between ingestive and masticatory toughness of foods. While the former is higher, the latter appears to have a closer relationship to the functional morphology of the masticatory apparatus, probably as a consequence of cyclical loading during chewing.

ACKNOWLEDGMENTS

I acknowledge Peter Lucas for being the inspirational leader of the Pantropical Primate Project (PPP) and for critical discussion of this paper. I thank the members of the PPP, and especially Mary Blanchard for her able assistance in the field, and P.Y. Cheng. Andriamihaja Benjamin and the staff of the Institute for Conservation of Tropical Environments, and Ratsirarson Joel, greatly facilitated this study. Permission to conduct this research was given by Association Nationale pour la Gestation des Aires Protégées, the Département des Eaux et Fôret, and the Université d'Antananarivo in Madagascar. Many thanks go to the staff and families at Beza Mahafaly reserve, and especially Ravolololonjatovo Lanto and Ravelonjatovo Sylvia. Lahavelo and Richard Corlett helped with plant identification. I am indebted to Alison Richard and Bob Sussman for censusing the lemurs at Beza Mahafaly. The comments of two reviewers improved the quality of the paper.

APPENDIX. Plant species, parts tested, and locations on plants used in toughness tests

Plant species	Family	Vernacular name	Ingestive position[1]	Plant part	Ingestive R^2		"Average" R^2	
					Number[3]	Where tested	Number[3]	Where tested
Propithecus v. verreauxi								
Acacia bellula	Fabaceae	Tratriotsy	1, 2, 3	Leaves	7	Rachis	6	Pinnule
		Tratriotsy	1	Flower	3	Stalk	1	Filament
Acacia rovumae	Fabaceae	Robontsy	1, 3	Leaves	15	Pinnae	15	Pinnule
Acacia sp.	Fabaceae	Roi	3	Leaves	3	Rachis	3	Pinnule
		Roi	3	Flower	1	Peduncle	1	Nectary
Acacia sp.?	Fabaceae	Hafotse ampelambatose	2	Leaves	1	Rachis	1	Pinnule
Albizia sp.	Fabaceae	Halimboron'ala	1, 2	Leaves	3	Rachis	3	Pinnule
Alchoornea sp.	Euphorbiaceae	Tagnatagna	1	Leaves	1	Leaf base	1	Midleaf
Anacolosa pervilleana	Olacaceae	Tanjaka	2	Leaves	3	Leaf base	3	Midleaf
		Tanjaka	1	Fruit	2	Mesocarp		
Arbrus precatorus	Papillioniaceae	Voamena	2	Leaves	5	Rachis	5	Pinnule
Azima tetracantha	Salvadoraceae	Filofilo	1	Fruit	2	Through fruit[4]	2	Through fruit[4]
Bridelia pervilleana	Euphorbiaceae	Hary	3	Leaves	5	Leaf base	5	Midleaf
Calopixis eriantha	Combretaceae	Tamenake	2	Stalk	1	Stalk		
Cedrelopsis grevei	Meliaceae	Katrafay	2, 3	Leaves	4	Mid-lf, petiole	4	Midleaf
		Katrafay	1	Flower	4	Peduncle	4	Flower bud
		Katrafay	2, 3	Stalk	3	Petiole	3	Petiole
		Katrafay	1, 2	Shoot	5	Stalk	5	Shoot tip
Commiphora aprevalii	Burseraceae	Daro	2	Leaves	4	Rachis	4	Pinnule
Commiphora brevicalyx	Burseraceae	Taraby	1	Leaves	2	Midleaf	2	Midleaf
Commiphora simplicifolia	Burseraceae	Tsingatse	1	Fruit	1	Through fruit	1	Through fruit
Crateva excelsa	Capparaceae	Akaly	2	Leaves	2	Leaf base	2	Midleaf
Dialium madagascariense	Fabaceae	Karimbola mitsy	1	Leaves	1	Mid-leaf	1	Midleaf
Dichrostachys humbertii	Fabaceae	Avoha	1, 3	Leaves	23	Rachis	25	Pinnules
		Avoha	2	Fruit	2	Pod	2	Pod
Euphorbia tirucalli	Euphorbiaceae	Famata	2, 3	Stalk	17	Stalk	16	Stalk tip
		Famata	1, 3	Fruit	4	Stalk	4	Through fruit
Gonocrypta grevei	Asclepiadaceae	Kompitse	1, 2, 3	Leaves	12	Leaf base	12	Midleaf
Grewia grandidieri	Tiliaceae	Sele bohoke	2	Leaves	1	Leaf base	1	Midleaf
Grewia grevei	Tiliaceae	Kotipoke	3	Leaves	9	Leaf base	9	Midleaf
		Kotipoke	2	Fruit	1			
Grewia triflora	Tiliaceae	Sele	2	Leaves	10	Leaf base	10	Midleaf
Grewia sp.	Tiliaceae	Malimatse	1	Fruit	1			
Grewia sp.	Tiliaceae	Maintyfototse	1, 3	Leaves	10	Leaf base	10	Midleaf
Landolphia sp.	Apocynaceae	Pira	3	Leaves	1	Stalk	1	Midleaf
Marsdenia cordifolia	Asclepiadaceae	Bokabe	1, 2, 3	Leaves	8	lf base, stalk tip	8	Midleaf
Metaporana parvifolia	Convolvulaceae	Kililo	1, 3	Leaves	16	Petiole	17	Midleaf
Pentopetia sp.	Asclepiadaceae	Tsompia	2	Leaves	3	Leaf base	3	Midleaf
Phyllanthus seyrigii	Euphorbiaceae	Sagnira	2	Leaves	2	Leaf base	2	Midleaf
Physena sessiliflora	Capparaceae	Fandriandambo	1, 2, 3	Leaves	20	Leaf base	20	Midleaf
Quivisianthe papinae	Meliaceae	Valiandro	3	Leaves	1	Leaf base	1	Midleaf
		Valiandro	1	Flower	5	Peduncle	5	Flower bud
Rhopalocarpus lucidus	Sphaerosepalaceae	Tsiongake	1, 2	Leaves	6	Leaf base	6	Midleaf
Roupellina boivinii	Apocynaceae	Sabonto	2	Leaves	7	Leaf base	7	Midleaf

Continued

Plant species	Family	Vernacular name	Ingestive position[1]	Plant part	Ingestive R^2		"Average" R^2	
					Number[3]	Where tested	Number[3]	Where tested
Salvadora augustifolia	Salvadoraceae	Sasavy	2	Stalk	1	Proximal stalk	1	Midstalk
Secamone sp.	Asclepiadaceae	Angalora	3	Leaves	2	Leaf base	2	Midleaf
Talinella dauphinensis	Portulacaceae	Dango	1, 2, 3	Leaves	9	Leaf base	9	Midleaf
		Dango	1	Flower	1	Peduncle	1	Pedicel
Tamarindus indica	Fabaceae	Kily	3	Leaves	3	Pinnae	3	Pinnule
		Kily	1, 2, 3	Fruit	10	Shell		
		Kily	1, 3	Flower	8	Stem	8	Flower parts
Tamelapsis linearis	Asclepiadaceae	Tamboro	1, 2	Leaves	4	Leaf base	4	Midleaf
Terminalia fatrae	Combretaceae	Talifatra	1, 3	Leaves	6	Mid-lf; lf base	6	Midleaf
Terminalia mantali	Combretaceae	Taly	1, 2, 3	Leaves	7	Leaf base	7	Midleaf
		Taly	1, 3	Fruit	3	Through "leaf"	3	Through fruit
Terminalia seyrigii	Combretaceae	Talivorokoko	1	Leaves	2	Lf base; stem	2	Midleaf
		Armed tree	1	Leaves	1	Midleaf	1	Midleaf
		Latex vine	1, 2	Leaves	4	Leaf base	4	Midleaf
		Large common ground vine	2, 3	Leaves	4	Leaf base	4	Midleaf
		Roimaintyfototse	1, 3	Leaves	3	Leaf base	3	Midleaf
		Sarivagnemba	2	Leaves	1	Petiole	1	Midleaf
		Sarivagnemba	1, 3	Flower	4	Peduncle	5	Flower bud
		Sarivagnemba	3	Fruit	3	Pod	3	Pod
		Tsianagnampo	2	Leaves	1	Leaf base	1	Midleaf
		Unktree 1	2	Leaves	1	Leaf base	1	Midleaf
		Unktree 2	1	Leaves	3	Leaf base	3	Midleaf
		Unkvine	1	Leaves	2	Leaf base	2	Midleaf
		Varo	1	Flower	1	Peduncle	1	Nectary
Lemur catta								
Acacia bellula	Fabaceae	Tratriotsy	1	Leaves	1	Rachis	1	Pinnule
Azima tetracantha	Salvadoraceae	Filofilo	1	Fruit	4	Through fruit	4	Through fruit
Cedrelopsis grevei	Meliaceae	Katrafay	1, 2	Leaves	5	Lf base; pinnae	5	Mid-lf; pinnule
Clerondendrum sp.	Verbenaceae	Forimbitike	2	Leaves	2	Leaf base	2	Midleaf
Combretum albiflorum	Combretaceae	Taritarike	1	Flower	2	Peduncle	1	Bud
Commelina sp.	Commelinaceae	Andranahaka	2	Stalk	1	Stalk	1	Stalk
Dioscorea sp.	Dioscoreaceae	Oxiala	1	Leaves	1	Leaf base	1	Midleaf
Enterospermum pruinosum	Rubiaceae	Mantsake	1	Fruit	1	Mesocarp	1	Mesocarp
Euphorbia tirucalli	Euphorbiaceae	Famata	2	Stalk	1	Stalk		
Gonocrypta grevei	Asclepiadaceae	Kompitse	2	Leaves	1	Leaf base	1	Midleaf
Grewia leucophylla	Tiliaceae	Tratraborondreo	1	Fruit	1	Mesocarp	1	Mesocarp
Grewia sp.	Tiliaceae	Malimatse	1	Fruit	1			
Maerua filiformis	Capparaceae	Soamangy	1	Flower	1	Needle	1	Bud
Marsdenia cordifolia	Asclepiadaceae	Bokobe	2, 3	Leaves	5	Lf base, stalk tip	4	Midleaf
Metaporana parvifolia	Convolvulaceae	Kililo	1, 2, 3	Leaves	33	Petiole	33	Midleaf
Pentopetia sp.	Asclepiadaceae	Tsompia	2	Leaves	2	Leaf base	2	Midleaf
Quivisianthe papinae	Meliaceae	Valiandro	1	Flower	4	Peduncle	4	Bud
Salvadora angustifolia	Salvadoraceae	Sasavy	1, 3	Leaves	3	Petiole	3	Midleaf
		Sasavy	1	Fruit	1	Through fruit	1	Through fruit
Talinella dauphinensis	Portulacaceae	Dango	1, 3	Leaves	8	Leaf base	8	Midleaf
		Dango	2, 3	Stalk	5	Stalk		
Tamarindus indica	Fabaceae	Kily	1, 2, 3	Leaves	14	Rachis	14	Pinnule
		Kily	2	Fruit	25	Shell		
		Kily	1	Flower	3	Stem	3	Flower parts
Terminalia fatraea	Combretaceae	Fatra	2	Fruit	1	Through fruit	1	Through fruit
		Fatra	2	Flower	1	Nectary	1	Flower parts
Tragia tiverneana	Euphorbiaceae	Sagnatry	1	Leaves	2	Petiole	2	Midleaf
		Bea	2	Leaves	3	Leaf base	3	Midleaf
		Bigfuzlf	3	Leaves	1	Petiole	1	Midrib
		"Clematis" vine	1	Leaves	1	Leaf base	1	Midleaf
		"Clematis" vine	3	Shoot	3	Petiole	3	Midleaf
		Large common ground vine	2, 3	Leaves	2	Petiole	2	Midleaf
		Lisinamboa	2	Leaves	4	Midleaf	4	Midleaf
		Rivervine	1, 2, 3	Fruit	5	Mesocarp	5	Mesocarp
		Sarirotsy	2	Fruit	1	Fruit peel	2	
		Saritoboara	1	Fruit	2			
		Teloravy	2	Leaves	2	Midleaf	2	Midleaf
		Tsinaikibo	1	Leaves	1	Midleaf	1	Midleaf
		Unkshrub	1	Flower	1	Stem		
	Convolvulaceae	Velae	1, 3	Flower	3	Nectary	3	Flower parts
		Vine	1	Leaves	1	Petiole	1	Midleaf

[1] 1, anterior; 2, posterior; 3, combination.
[2] Ingestive R, maximum toughness values; "Average" R, average toughness values; Mid-lf, midleaf; Lf, leaf. See text for further explanation.
[3] Denotes number of times each species was tested through course of year; 3–4 plant parts were tested for each plant species.
[4] "Through fruit" means that the entire fruit was placed on scissor blades and cut. Seeds were not included in the cut.

LITERATURE CITED

Agrawal KR, Lucas PW, Bruce IC, Prinz JF. 1998. Food properties that influence neuromuscular activity during human mastication. J Dent Res 77:1931–1938.

Coimbra-Filho AF, Mittermeier RA. 1976. Exudate-eating and tree-gouging in marmosets. Nature 262:630.

Darvell BW, Lee PKD, Yuen TDB, Lucas PW. 1996. A portable fracture toughness tester for biological materials. Meas Sci Technol 7:954–962.

Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evol Anthropol 10:171–186.

Gordon JE. 1976. The new science of strong materials, or why you don't fall through the floor, second edition. Harmondsworth, UK: Penguin Books, Ltd.

Happel R. 1988. Seed-eating by West African cercopithecines, with reference to the possible evolution of bilophodont molars. Am J Phys Anthropol 75:303–327.

Hiiemae KM, Crompton AW. 1985. Mastication, food transport and swallowing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge: Belknap Press. p 262–290.

Hylander WL. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science 189:1095–1097.

Hylander WL. 1979. The functional morphology of primate mandibular form. J Morphol 160:223–240.

Iwano T, Iwakawa C. 1988. Feeding behaviour of the aye-aye (*Daubentonia madagascariensis*) on nuts of ramy (*Canarium madagascariensis*). Folia Primatol (Basel) 50:136–142.

Izawa K, Mizuno A. 1977. Palm-fruit cracking behavior of wild black-capped capuchin *(Cebus apella)*. Primates 18:773–792.

Jablonski NG, Crompton RH. 1994. Feeding behavior, mastication, and tooth wear in the western tarsier (*Tarsius bancanus*). Int J Primatol 15:29–59.

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

Kiltie RA. 1982. Bite force as a basis for niche differentiation between rain forest peccaries (*Tayassu tajacu* and *T. pecari*). Biotropica 14:188–195.

Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. Am J Phys Anthropol 81:5–15.

Kinzey WG, Rosenberger AL, Ramirez M. 1975. Vertical clinging and leaping in a neotropical anthropoid. Nature 255:327–328.

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p 173–203.

Lucas PW, Corlett RT, Luke DA. 1986. Postcanine tooth size and diet in anthropoid primates. Z Morphol Anthropol 76:253–276.

Lucas PW, Choong MF, Tan HTW, Turner IM, Berrick AJ. 1991. The fracture toughness of the leaf of the dicotyledon *Calophyllum inophyllum* L. (Guttiferae). Philos Trans R Soc Lond [Biol] 334:95–106.

Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orang-utans with their teeth in captivity and a new technique for estimating forces produced in the wild. Am J Phys Anthropol 94:365–378.

Lucas PW, Teaford MF, Ungar PS, Glander KE. 1998. Physical properties of foods in *Alouatta palliata*. Am J Phys Anthropol [Suppl] 26:152 [abstract].

Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000. Mechanical defenses to herbivory. Ann Bot 86:913–920.

Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee PKD, Osorio D, Ramsden L, Yamashita N, Yuen TDB. 2001. Field kit to characterize physical, chemical and spatial aspects of potential primate foods. Folia Primatol (Basel) 72:11–25.

Marchant L, McGrew W. 2002. Percussive technology: wild chimpanzees pound open baobab fruits. Am J Phys Anthropol [Suppl] 34:106–107 [abstract].

Milton K. 1978. Role of the upper canine and P^2 in increasing the harvesting efficiency of *Hapalemur griseus* Link, 1795. J Mamm 59:188–190.

Nash LT. 1986. Dietary, behavioral and morphological aspects of gummivory in primates. Yrbk Phys Anthropol 29:113–138.

Niklas KJ. 1992. Plant biomechanics. Chicago: University of Chicago Press.

Peres CA. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazonia. Biotropica 23:262–270.

Ravosa MJ. 1991. Structural allometry of the prosimian mandibular corpus and symphysis. J Hum Evol 20:3–20.

Santini-Palka M-E. 1994. Feeding behaviour and activity patterns of two Malagasy bamboo lemurs, *Hapalemur simus* and *Hapalemur griseus*, in captivity. Folia Primatol (Basel) 63:44–49.

Schwartz JH, Tattersall I. 1985. Evolutionary relationships of living lemurs and lorises (Mammalia, Primates) and their potential affinities with European Eocene Adapidae. Anthropol Pap Am Mus Nat Hist 60:1–100.

Strait SG. 1997. Tooth use and the physical properties of food. Evol Anthropol 5:199–211.

Ungar PS. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. Am J Phys Anthropol 95:197–219.

Yamashita N. 1996. Seasonality and site-specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). Int J Primatol 17:355–387.

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

Yamashita N. 2002. Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. Int J Primatol 23: 1025–1051.