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It's Tough Out There: Variation in the Toughness of Ingested Leaves and Feeding Behavior Among Four Colobinae in Vietnam

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Abstract Colobines are similar in their exploitation of a high percentage of leaf matter. However, this observation obfuscates interesting differences among genera of Southeast Asian colobines in morphology and behavior that may be reflected in the degree to which they rely on mastication or gut volume and gut retention time when ingesting and digesting leaves. We detail the use of a laboratory-based method to measure the mechanical properties of foods selected and processed by 4 captive species of Southeast Asian Colobinae —*Pygathrix nemaeus*, *Pygathrix cinerea*, *Trachypithecus delacouri*, and *Trachypithecus laotum hatinhensis*— at the Endangered Primate Rescue Center (EPRC), Vietnam. We also detail a field method that quantifies chewing rates and chewing behavior via a consumer-grade video camera and laptop computer. Observations in the captive setting permit a degree of experimental control that is not possible in the wild, and the location of the EPRC in the primates' habitat country permitted us to provide leaves that they encounter and eat in the wild. We collected toughness data with a portable tester designed by Lucas *et al.* The average toughness of selected leaves does not differ among the taxa, nor does the length of time spent chewing foods. However, there are differences in feeding rate, with *Trachypithecus* spp. chewing foods twice as fast as *Pygathrix* spp. Our findings suggest that *Trachypithecus* spp. emphasize comminution of food by mastication, while *Pygathrix* spp. emphasize the comminution of leaf matter

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in the stomach. The hypothesis is supported by data on molar size, gut mass, and gut morphology. We provide new insights into dietary variation among primate species and detail methods that are typically conducted only in a laboratory setting. We augment the findings with additional data on activity, feeding rates, and tooth morphology.

Keywords chewing rates · food material properties · portable mechanical tester · Southeast Asian colobines · toughness

Introduction

Vietnam contains 10 species of leaf-eating primates representing 3 genera (Nadler *et al.* 2004). Though dietary data on the primates are limited, researchers have hinted at ecomorphological relationships among diet, feeding behavior, craniodental morphology, and gut physiology in these highly endangered colobines (Caton 1998; Jablonski *et al.* 1998; Kirkpatrick 1998). Over the past decade data have accumulated that demonstrate a relationship between the dental and cranial morphology of leaf-eaters and the average toughness of their diets in the wild. For example, Wright (2005) showed that the average toughness of foods masticated by howlers exceeds that of 5 other platyrrhine taxa in a primate community in central Guyana. Howlers exhibit well developed crests on large molars that make the comminution of tough foods more effective and time efficient (Lucas 2004; Rosenberger 1992).

Members of the Colobinae exhibit well-developed crests on their teeth and sacculation of the gut, which do not occur in other behavioral folivores, e.g., howlers and gorillas (Caton 1998, 1999; Fleagle 1999; Jablonski *et al.* 1998). Though researchers have documented a high percentage of leaf consumption in members of the Colobinae, my colleagues and I made initial qualitative observations of the morphology and ecology of leaf-eating monkeys in Vietnam that suggested differences among the primates in the way they process leaves to extract required nutrients. We compare the ingestive and digestive strategies of 2 genera of Vietnam leaf monkeys. We include 2 species of *Trachypithecus* (limestone langurs) and 2 species of *Pygathrix* (douc).

Is there more than one way to eat a leaf?

Leaves demand both mechanical and chemical mechanisms for the extraction of water and nutrients (Cheng *et al.* 1980; Dominy *et al.* 2001; Lucas *et al.* 1995). For mammals to gain required nutrients from leaves, they must be exposed to microbes that convert structural and nonstructural carbohydrates initially into monosaccharides and disaccharides and ultimately into volatile fatty acids (Cheng *et al.* 1980; Van Soest 1994, Waterman and Kool 1994). The effectiveness of the process can be influenced in 3 primary ways: 1) by retaining the leaves in the gut for extended periods, thus permitting longer exposure to gut fauna; 2) by expanding the gut and permitting more food to be digested at any one time; and 3) by increasing the surface area for the microbes to act upon by breaking leaves into smaller pieces via mastication (Lucas *et al.* in prep). Reptiles exhibit adaptations permitting the first 2 methods (Pafilis *et al.* 2007: gut retention; O'Grady *et al.* 2005: gut morphology). Birds also exhibit variation in gut retention times (Fukui 2003) and morphology

(Battley and Theunis 2005; Grajal *et al.* 1989), and some exhibit adaptations of the bill and hyoid bone for food processing (Korzoun *et al.* 2003). Like birds, primates and other mammals exhibit gut and oral adaptations, particularly dental adaptations, to ingest and to digest foliage (Lucas 2004). But this begs the question: Do folivorous animals, particularly primates, emphasize any of these methods to the exclusion of others, and does the emphasis on any one method differ among closely related species? By holding dietary toughness constant, we sought to identify the degree to which *Pygathrix* spp. and *Trachypithecus* spp. are dependent on the mastication of leaves before digestion in the gut. We augment our findings by comparing size-adjusted molar areas between them and by a review of literature on variation in gut size and morphology among them.

Dietary Toughness and its Selective Influence on Primate Morphology and Masticatory Behavior

Toughness is the energy consumed in propagating a crack of a given area and is measured as the area under a force-displacement curve divided by crack area (Ashby 1992; Lucas 2004; Vincent 1992). During mastication, fragmentation of food between the teeth is largely dependent on either toughness or a combination of toughness and stiffness, and can be expressed as fragmentation indices (Agrawal *et al.* 1997; Lucas *et al.* 2002; Williams *et al.* 2005). Food tissues that can withstand high strains before crack propagation are termed displacement limited (Lucas *et al.* 2000) and demand such adaptations as well-developed crests on the postcanine dentition. Leaves are the quintessential displacement-limited foods in the diets of primates. Toughness alone is a good indicator of the mechanical demands that they place on the masticatory system, particularly among colobines, which are relatively dependent on leaves. Colobine primates exhibit relatively large molars, which increases the degree to which foods are comminuted per chew, and they exhibit crests that assist in driving cracks through tough materials, much the way scissors cut through paper (Lucas 2004).

We adapted laboratory equipment and software to field conditions to permit measurement of dietary mechanics. We acquired leaf toughness data via a portable field tester. We collected data on chewing bout lengths and chewing rates via a consumer-grade camera and videotape digitizing software.

Methods

Dietary Toughness

By providing the primates with monospecific bundles of leaves, we ranked the most preferred, moderately preferred, and least preferred foods. The portable universal tester we used was initially designed for testing the mechanical properties of foods processed by primates, and has been refined by Lucas and Darvell along with collaborators at the University of Hong Kong (Darvell *et al.* 1996; Lucas *et al.* 2001). The tester (Fig. 1), which is similar to Instron™ machines used in mechanical tests of larger or more mechanically demanding objects, is comprised of 3 essential components: 1) the stainless steel test stand, which is host to 1 of 2 load cells with limits of 10 and 100 Newtons

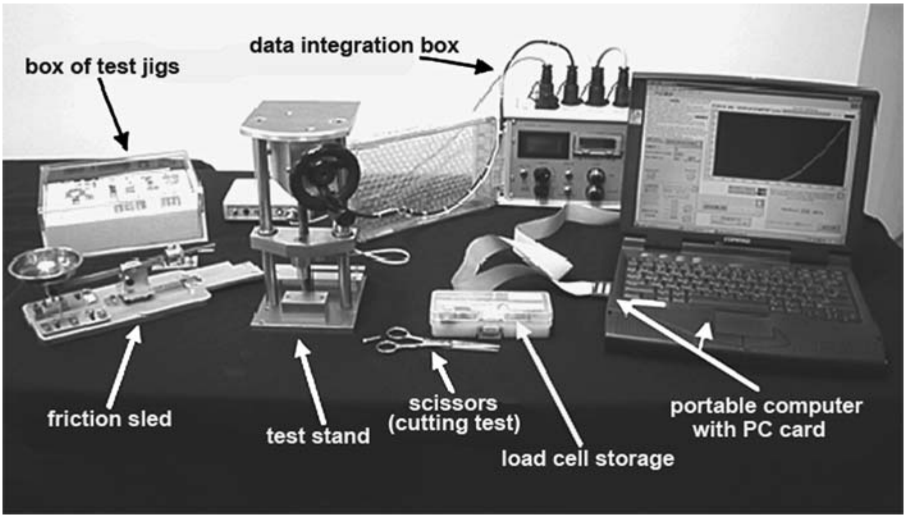


Fig. 1 Photo of the mechanical test stand, integration box, and computer used for the collection of toughness data. Accessories for a range of different mechanical tests are labeled. Photo courtesy P.W. Lucas.

(the load cells are sensitive enough to measure the stress-strain ratio of extremely small deformations); 2) the data integration box, which measures force in compression or tension and also displacement of the stand's crosshead to which the load cell is attached; and 3) a portable computer with software to read the output from the integration box. Toughness in Joules/m^2 is provided after one enters the force in Newtons for a cut of a given area (length and depth) into the computer. Scissor tests control fracture, making them particularly reliable, consistent, and relatively versatile. All reported tests are of toughness derived from scissor tests. One can test toughness in wedging and measure Young's modulus (stiffness) also by compressing or bending specimens, and obtain the coefficient of friction via a weighted sled device. We conducted 2 sample comparisons via the Mann-Whitney *U* test between the 2 genera for the toughness of foods in each preference category and for all foods combined (Table I). We chose a nonparametric test statistic owing to the increase in variance that occurs with increasing food toughness (Williams *et al.* 2005).

Table I Sample sizes for toughness and chewing variables

Variable	*Pygathrix nemaeus*	*P. cinerea*	*Trachypithecus l. hatinhensis*	*T. delacouri*
Toughness all	53	51	51	53
Toughness high	17	15	15	17
Toughness mid	18	18	18	18
Toughness low	18	18	18	18
Chewing bouts	31	30	30	30
Chewing rates	21 (4–20)	24 (5–23)	19 (4–10)	20 (4–18)

The first number for chewing rates is the number of foods used for the analysis. The numbers in parentheses are the maximum and minimum number of chews we used to calculate chewing rate for each food.

Chewing Rates and Bout Lengths

We filmed subjects with a Sony Handycam high-speed consumer-grade camcorder while they were feeding. We imported video clips into Final Cut video software and converted them to Quicktime files (Table I). We did not conduct the video analysis on site, but it is possible given sufficient time. We measured chewing rates from watching lip and jaw movements onscreen, slowing the recordings if necessary to increase accuracy. Timing at any speed was possible because of the onscreen clock, which is synchronized with the video frames no matter the speed. We obtained chewing rate data at 4 different enclosures that housed 1 each of the 4 focal species (Table II). We took chewing rates randomly from various films and could not match them with leaf toughness; however, we paired feeding bouts with leaf toughness for additional analysis. We examined the video frame-by-frame to identify the beginning of feeding bout, end of ingestion phase/beginning of chewing phase, and end of feeding bout. Table I contains the number of bouts for each species and sex. We compared differences in feeding rates and in chewing bout lengths between the species and genera via the nonparametric Mann-Whitney *U* test statistic (the equivalent of the parametric 2-sample Student's *t* statistic).

Relative Molar Size and Observations

To augment the findings from the analyses of dietary toughness and feeding behavior, we measured the teeth of all 4 species at the National Museum of Natural History (NMNH) and at the Endangered Primates Rescue Center (EPRC), Vietnam. All 4 focal primates are either endangered (*Pygathrix nemaeus* and *Trachypithecus I. hatinhensis*) or highly endangered (*P. cinerea* and *T. delacouri*), which together with limited work by Western scientists throughout Southeast Asia through much of the 20th century, has limited the number of museum specimens. Our best represented species for the morphological analysis is *Pygathrix nemaeus* (n=11 NMNH, n=1 EPRC), followed by *P. cinerea* (n=6 EPRC), *Trachypithecus I. hatinhensis* (n=2, EPRC), and *T. delacouri* (n=1 EPRC). We pooled the species in each genus for analysis. We calculated a ratio of molar area (calculated from buccolingual and mesiodistal measurements of M_2) divided by cranial vault length (from nasion to opisthocranion) ×100 for each specimen to control for size. We used the Mann-Whitney *U* test to compare the ratios between the 2 genera. Tooth size scales with body mass, but we found no body mass datum for *Pygathrix cinerea*, *Trachypithecus I. hatinhensis*, or *T. delacouri*.

Table II Number of adult males and females in each study group that were included in the study

Species	Group structure
Pygathrix nemaeus	♀7; ♂8(est)
P. cinerea	♀ unknown; ♂ 12(est)
Trachypithecus I. hatinhensis	♀ unknown; ♂ 15(est)
T. delecouri	♀ 6; ♂ 12(est)

Age is provided after the symbol (est = age estimate for confiscated animals). Number of symbols in each cell = number of individuals for the given sex.

Results

Leaf Toughness

Mid-ranked leaves were the toughest tissues ingested by the 4 focal species (Table III). The subjects could have dealt with the least preferred items mechanically, but may have avoided doing so because of the presence of secondary chemical compounds. However, there is no significant difference between all pairs of leaf monkey for each preference category and for all leaf specimens pooled ($p>0.05$). Thus, it appears that when given the opportunity to exploit the same foods in the absence of interspecific competition, the focal species select foods of comparable toughness (Fig. 2). Thus, we can say with some certainty that toughness was held constant when observing chewing bout lengths and chewing rates.

Chewing Bouts

There is a significant difference between *Pygathrix cinerea* with the shortest bouts and *P. nemaeus* with the longest bouts (Table IV; Fig. 3) and there is a trend for increasing bout length with an increase in the toughness of ingested leaves (Fig. 4). However, there is no difference between *Pygathrix* and *Trachypithecus* for chewing bout length. The bout lengths for the 2 *Trachypithecus* spp. lie between those for *Pygathrix* spp.; thus no genus-wide pattern is apparent. Logan and Sanson (2002) found an increase in chewing bout length with an increase in dental wear in koalas. However, King *et al.* (2005) found that compensatory shearing blades occur up to the age of 18 in *Propithecus edwardsi*, after which the molars begin to lose their shearing capability. The age of our female *Pygathrix cinerea* is unknown; however, the age of the male *P. cinerea* (12 yr) exceeds that of the male *P. nemaeus* (8 yr) by *ca.* 4 yr (Table II). It may be that the shearing efficiency of the older male gray-shanked douc actually exceeds that of the younger male red-shanked douc given the findings of King *et al.* (2005), which may increase the degree of leaf comminution per unit time. However, the difference between the 2 genera is statistically negligible.

Chewing Rates

There are differences in chewing rate between the 2 primate genera and among the primate focal species (Table V; Fig. 5). *Trachypithecus* spp. (median=3.01 s^{-1}) ate

Table III Average toughness (J m^{-2}) of high-, middle-, and low-priority foods, eaten by all 4 focal species

Preference	*Pygathrix cinerea*	*P. nemaeus*	*Trachypithecus delacouri*	*T. l. hatinhensis*
High	**855.3**	733.1	673.0	799.9
Middle	**1305.9**	1169.5	1177.5	1155.8
Low	1031.1	1088.4	1007.9	**1107.8**
Max all eaten	**4937.6**	4093.0	3002.8	3195.9

The bottom row indicates the toughest tissues eaten by all 4 primates. The highest values are in bold type. There is no significant differences ($p>0.05$) in all species comparisons for all categories and all foods combined.

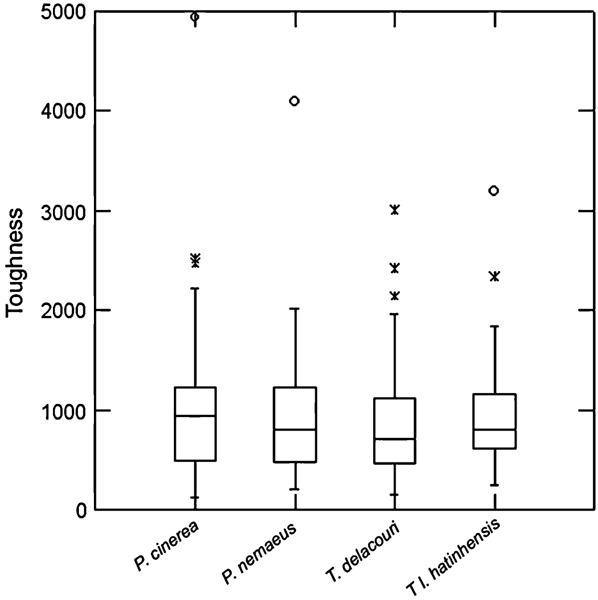


Fig. 2 Box-and-whisker plots of the toughness of ingested leaves for each of the 4 primates species in this study (Mann-Whitney U, $p > 0.05$ for all comparisons). Vertical line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles.

foods more quickly than *Pygathrix* spp. did (2.43 s^{-1}; $p < 0.01$). Among the 4 species, *Trachypithecus delacouri* (3.18 s^{-1}) chewed the quickest, and the rate is significantly higher than that for the other 3 species ($p < 0.01$). *Trachypithecus I. hatinhensis* (2.76 s^{-1}) process foods quicker than either *Pygathrix* spp. does (*P. namaeus*=2.47, *P. cinerea*=2.40), while the chewing rates for both *Trachypithecus* spp. are comparable ($p > 0.05$). To evaluate if faster chewing by *Trachypithecus* spp. was due to smaller less efficient molars we compared molar size among the focal species.

M_2 size

Given the small sample size for *Trachypithecus delacouri* (n=1) and *T. I. hatinhensis* (n=2), we pooled them for analysis of molar size (Fig. 6). The ratio of molar area to vault length for *Trachypithecus* (median=56.28) is significantly greater than that for

Table IV Mann-Whitney *U* test statistic results for chewing bout length for all species pairs

Chewing Bouts	*Pygathrix nemaeus* (5.91)	*P. cinerea* (2.96)	*Trachypithecus I. hatinhensis* (5.69)	*T. delacouri* (4.31)	*Trachypithecus* (5.05)
Pygathrix nemaeus	na				
P. cinerea	**$p < 0.01$**	na			
Trachypithecus I. hatinhensis	$p > 0.05$	**$p < 0.01$**	na		
T. delacouri	**$p = 0.05$**	**$p < 0.01$**	$p > 0.05$	na	
Pygathrix (3.78)					$p > 0.05$

The p value in the lower right corner is for the comparison between genera. Median chewing bout values are given with the genus and species designations.

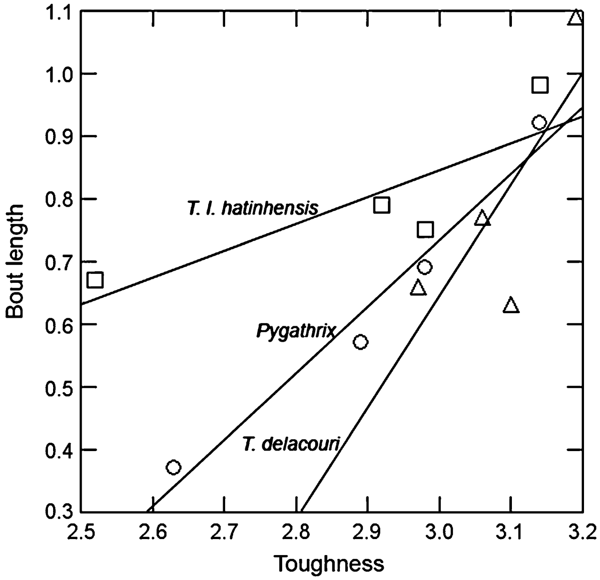


Fig. 3 Log transformed bout length (in seconds) linearly regressed against log transformed toughness (J m^{-2}) for the same food items for each primate species (*T. hatinhensis* = □, *Pygathrix* = ○. *T. delacouri* =△. The *pygathrix* species were pooled for analysis due to only one specimen of *P. nemaeus* (the largest value for *P. nemaeus* at 1371.2 J m^{-2}). Note the general trend for an increase in bout length with an increase in leaf toughness for each primate species.

the *Pygathrix* spp. (median=47.09). Though the sample sizes are small, the finding suggests that along with increased chewing rate, *Trachypithecus* increase the degree to which leaves are comminuted per chew.

Discussion

Our study revealed differences among a subset of Southeast Asian colobines in the way they process leaves of comparable toughness. Two distinct strategies emerge. *Trachypithecus* spp. depend more on high masticatory rates to increase comminution of foods before swallowing. This is predicted to increase the surface area of leaves on which microbes can act. It appears that increased chewing rates in the limestone langurs are combined with larger molars to increase the efficiency of leaf comminution per chew. *Pygathrix* spp. chew foods for the same amount of time as

Table V Mann-Whitney U test statistics for chewing rates (s^{-1}) for all species pairs

Chewing rates	*Pygathrix nemaeus* (2.47)	*P. cinerea* (2.40)	*Trachypithecus l. hatinhensis* (2.76)	*T. delacouri* (3.18)	*Trachypithecus* (3.01)
Pygathrix nemaeus	na				
P. cinerea	$p > 0.05$	na			
Trachypithecus l. hatinhensis	**$p < 0.01$**	**$p < 0.05$**	na		
T. delacouri	**$p < 0.01$**	**$p < 0.01$**	**$p < 0.01$**	na	
Pygathrix (2.43)					**$p < 0.01$**

The *p* value in the lower right corner is for the comparison between genera. Median rate values are given with the genus and species designations.

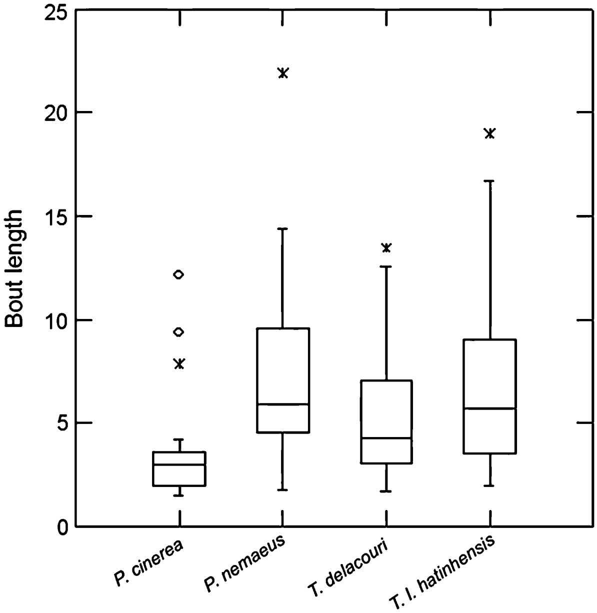


Fig. 4 Box and whisker plots of chewing bout length in seconds for each of the four primate species in this study (Mann-Whitney U, $p > 0.05$ between the two represented genera). Vertical line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles. Note the overlap among the species in both of the represented genera.

Trachypithecus spp. do, but they do not chew as quickly. In addition, their molars are smaller. Thus it appears that leaves enter the stomachs of the *Pygathrix* spp. in larger pieces. However, they may compensate for larger leaf size and less surface area per leaf by increasing stomach size and via the development of a presaccus. The stomach of *Pygathrix nemaeus* is 20% heavier than that of *Presbytis melalophos* (Caton 1998).

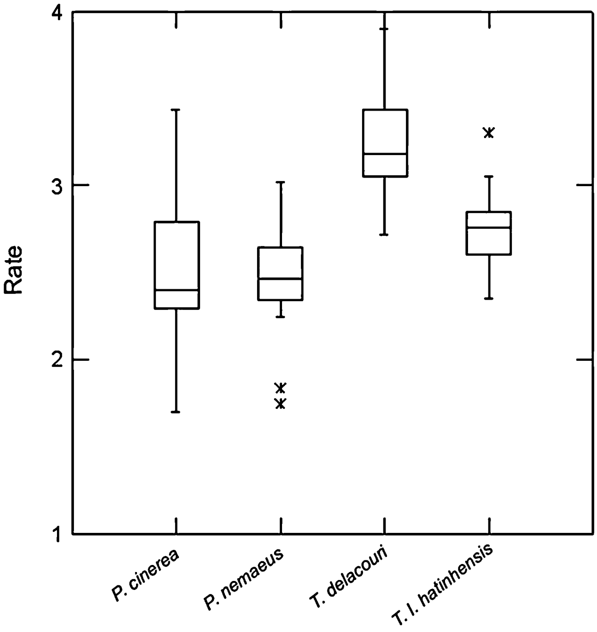
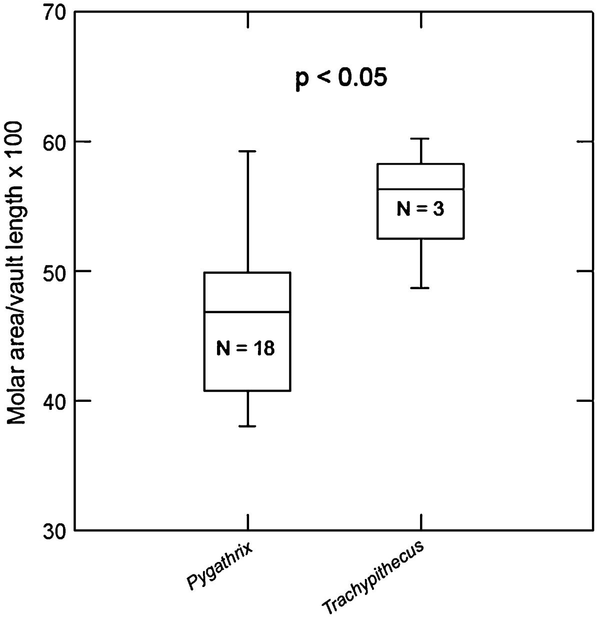


Fig. 5 Box and whisker plots of chewing rates (s^{-1}) for each of the four primate species in this study (Mann-Whitney U, $p < 0.01$ between the two represented genera). Vertical line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles. Note that the medians for both *Trachypithecus* species fall above those for both *Pygathrix* species.

Fig. 6 Box and whisker plots of molar area to cranial vault length ratios for the two primate genera in this study (Mann-Whitney U, $p<0.01$). Vertical line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles.



Further, the stomachs of *Pygathrix nemaeus*, like those of *Procolobus*, *Rhinopithecus*, and *Nasalis*, have a fourth stomach chamber: the presaccus (Caton 1998). The longitudinal muscle coat, squamous epithelial lining, and small size of the presaccus led Caton (1998) to suggest that the structure may be a gastric mill, breaking large ingested food particles into smaller pieces before passing them to the saccus. Though the stomachs of *Trachypithecus obscura* and *T. cristatus* exhibit 3 large chambers, they lack a presaccus (Caton 1999). However, they also exhibit an enlarged colic chamber similar to that in cercopithecines and apes, which may act as a secondary fermentation chamber (Caton 1999).

Our findings augment those of Caton (1998, 1999). The presacuss may play the role of additional ingestion and food particle comminution center in *Pygathrix* spp., thus permitting them to chew more slowly on smaller teeth. Lacking the presaccus, *Trachypithecus* spp. may rely more on oral comminution of foods, i.e. faster chewing rates and larger teeth, before exposure to microbes in a tripartite stomach.

We are unable to say whether one or the other system is actually more efficient in terms of energy and nutrient return per unit consumed leaf tissue. The lack of an additional colic digestive chamber in *Pygathrix* may be evidence of a more digestively efficient stomach, while seemingly lower activity levels in the genus suggest a less efficient total digestive system or a less calorically rich diet.

The energetics of positional behavior in the 2 genera differ in ways that demand further inquiry to relate directly to their patterns of food ingestion and digestion. *Trachypithecus* spp. exhibit higher percentages of leaping and quadrupedal walking than *Pygathrix* spp. do, while *Pygathrix* spp. suspend more frequently during foraging and locomotion than *Trachypithecus* spp. do (Stevens *et al.* 2008). Brachiation, when done in such a way that collisional energy loss is minimized, may be more energy efficient than initially argued in the primate literature (Bertram 2004), suggesting that the digestive strategy of *Pygathrix* may be less calorically efficient than the ingestive strategy of *Trachypithecus*. In addition, *Pygathrix* spp. are relatively less active than *Trachypithecus* spp. are (K. Wright *et al.*, in prep).

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