Feeding and oral processing behaviors of two colobine monkeys in Tai Forest, Ivory Coast.

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Abstract

We collected frequency data on oral processing behaviors during feeding in habituated groups of Western red colobus, *Piliocolobus badius*, and Western black and white, *Colobus polykomos*, ranging in the Ivory Coast's Tai National Park. During the sampling period, the diet of red colobus consisted of approximately 75% leaves compared to approximately 47% leaves and buds in black and white colobus. Black and white colobus chewed more frequently per ingestive event than did red colobus. Black and white colobus also employed their anterior teeth much more frequently than did red colobus, a difference attributed to the frequent consumption by *C. polykomos* of *Pentaclethra macrophylla* seeds and pods. A material analysis of these food items reveals that both the seed coating and seed flesh are quite soft; however, the pod housing the seeds is very tough. We argue that the pod's toughness, geometry, and fiber orientation collectively result in a food that is very difficult to process, resulting in long handling times and frequent, aggressive use of the incisors. We compare these data with those collected on another Tai primate—the sooty mangabey, *Cercocebus atys*—and demonstrate that during feeding, both colobine species use their incisors less than the mangabey, but that the cercopithecine chews less than either colobine. Combining data on oral processing behaviors with those on the material properties of items being ingested should lead to more informed interpretations of dentognathic morphology.

Introduction

The African colobines are allocated to three genera: the five species of black and white colobus are assigned to *Colobus*, *Piliocolobus* contains the seventeen red colobus species, and *Procolobus* houses the monotypic olive colobus (Fleagle, 2013). The feeding ecologies of African colobus monkeys have been the focus of numerous field studies; several species have been studied at multiple localities and groups of at least one species have been examined at one site over multiple decades (Struhsaker and Oates, 1975; Chapman et al., 2000; Chapman and Chapman, 2002). The accumulation of data indicates that while all African colobines consume significant quantities of leaves, there is important dietary variation among genera, species, and populations (Struhsaker, 2010; Davies and Oates, 1994; Fashing, 2011). The causes and consequences of feeding differences have been used to explain many aspects of colobine natural history including social structure, group size, ranging behavior, habitat use, predator avoidance, and, to some extent, craniodental morphology (e.g., Struhsaker and Oates, 1975; Struhsaker and Leland, 1979; Hayes et al., 1996; Davies et al., 1999; Fashing 2001; Korstjens et al., 2007; Chapman and Chapman, 2000).

Recognizing the significant inter- and intra-specific variation in food consumption, some basic dietary distinctions can be drawn between the three groups of African colobus. In a recent review, Fashing (2011) noted that while most red colobus monkeys (*Piliocolobus*) are primarily folivorous, they consume fewer mature leaves than do *Colobus* spp., preferring instead new leaves as well as ripe fruit, shoots, and flowers. West African red colobus especially eat significant quantities of fruit and seeds. The diets of black and white colobus monkeys (*Colobus*) are also dominated by leaves, but with greater consumption of mature leaves. Black and white colobus also eat large quantities of unripe fruit and seeds, and several populations are known to be highly granivorous. For example, Dasilva's study of *Colobus polykomos* at Sierra Leone's Tiwai Island highlighted the importance of *Pentoclethra macrophylla* seeds, a food that

figured prominently in discussions of energy expenditure, activity budget, and posture (Dasilva, 1992, 1994). Olive colobus monkeys (*Procolobus*) have the least variable diet, one that includes large quantities of young leaves.

The Ivory Coast's Tai Forest contains a representative of each African colobine genus and groups of these species have been under more or less continual study since the early 1990s. The three species are *Piliocolobus badius*, the Western red, Upper Guinea red, or Bay colobus; *Colobus polykomos*, the Western black and white, Western Pied, Ursine or King colobus; and *Procolobus verus*, the olive colobus. Long-term feeding data indicate that red colobus have the most diverse diet of the Tai colobines, one that consists of large quantities of young leaves, fruit, and flowers (Wachter et al., 1997; Korstjens, 2001; Korstjens et al., 2002). Tai's black and white colobus have a more restricted diet consisting of mature leaves supplemented with smaller amounts of fruit. An important difference obscured by use of the gross category "fruit" is that of seed consumption: red colobus at Tai typically consume fleshy fruits that are ingested whole, while black and white colobus feed more on seeds extracted from woody plants that lack fruit flesh (Korstjens et al., 2007).

Previously, we used the ingestive and processing demands of hard seed consumption as one basis for interpreting variation in the mandibular dimensions of *C. polykomos* and *P. badius* at Tai (Daegling and McGraw 2001). *C. polykomos* at Tai, like those at Tiwai, consume large quantities of *Pentaclethra macrophylla* seeds when they are available, typically between July and December (Dasilva, 1994; Oates and Davies, 1994; Schaaff, 1995; Korstjens, 2001). In the most extensive study of colobine feeding at Tai, Korstjens (2001) determined that when it is available, *P. macrophylla* fruit was the most frequently consumed food of *C. polykomos*, accounting for 12.7% of its annual diet. During those months of Korstjens' study when *P. macrophylla* was eaten, monthly contributions ranged from 6.4% (July) to 54.7 (September). *P. macrophylla* seeds are flat, disc-shaped foods about the size of a quarter and housed inside large, boomerang-shaped woody pods. We assumed (but did not test) that because the seeds were hard,

their frequent consumption by *C. polykomos* involved the generation of high bite forces and that resulting increased stresses would be reflected in more robust mandibular dimensions of *C. polykomos* compared to *Piliocolobus badius*, which do not consume this food.

Despite the advantage of having a skeletal sample derived from the same population as the feeding data, several of our results did not conform to predictions generated from biomechanical theory. We are not the first to have met with limited success in interpretations of craniodental form and feeding. In a recent review, Ross and colleagues (2012) lamented the efforts of other researchers who have attempted to relate mandibular form to diet and concluded that despite the increased statistical rigor, more detailed field studies, and advances in analytical techniques, the fit between mandibular geometry and gross characterizations of diet remains poor. These authors go on to highlight the importance of collecting information on feeding behavior rather than simply food categories, and argue that particular attention should be directed at how and how frequently animals ingest and process foods of varying material properties. These authors conclude that “...variation in primate diets is associated with variation in mandibular morphology only when there is also variation in feeding behavior that produces variation in loading regimes acting on the mandible” (Ross et al., 2012:654).

We enthusiastically agree and admit that while dietary variation in the Tai colobines is well documented, we have only a rudimentary understanding of feeding behavior as it pertains to ingestion and processing. Further, we lack information on the material properties of any colobine food. The importance of these omissions was underscored when micro-indentation experiments revealed significant variation in the elastic modulus of mandibular bone in the two Tai colobines (Daegling et al., 2009). These data indicated that symphyseal bone in *P. badius* was stiffer than that of *C. polykomos*, which led to the hypothesis that the demands of processing *P. macrophylla* fruits required that *C. polykomos* generate large masticatory forces and that the more compliant mandibular bone in black and white colobus was an adaptation for making bone tougher. Tougher bone is argued to be advantageous in contexts in which limiting microcrack growth, relative to maintaining material stiffness, is the more critical consideration. Specifically,

toughening bone by making it more compliant mitigates stress at the cost of allowing strain to increase, which promotes better energy-absorbing capacity of bone tissue. Whether this might be expected in contexts where bone is subjected to repeated ingestive or masticatory stress remains an open question. In any case, since we did not know how and how often the two colobine species chewed different foods (daily masticatory cycles), alternative hypotheses remained untested.

Consequently, studies of Tai colobines have been limited by incomplete understanding of how, how often, and in what context (i.e., food item consumed) different species employ their dentition and mandibles. Moreover, because no food material property data had been collected, we could not address the extent that variation in behavior required to consume different foods is responsible for shaping mandibular structure. Recent studies suggest that integrating these kinds of datasets has greater explanatory power than using more traditional diet categories. This approach has been applied to another Tai primate—the sooty mangabey *Cercocebus atys*—and proven useful in addressing several themes on the evolution of feeding morphology and behavior (Daegling et al., 2011c; McGraw et al., 2011, 2012).

Here we present data on incising and mastication during feeding for *P. badius* and *C. polykomos* in the Ivory Coast's Tai Forest. We consider both incision and mastication oral processing behaviors and our general question is: are there are inter-specific differences in incising and mastication (chewing) frequencies? In the course of the field study, it was determined that one food eaten by *C. polykomos* accounts for the major differences in oral processing behaviors between monkey species and we, therefore, present a material property analysis of the pods and seeds of this food to address the extent that variation in ingestive behavior is interpretable in terms of the structure of this dietary item. We proceed under the general null hypothesis that the food processing activities of red colobus and black and white colobus are identical and that the taxa employ similar frequencies of incising and masticating (i.e., chewing cycles).

Methods

Food processing behavior

We collected data on feeding and oral processing activities of red colobus (Fig. 1) and black and white colobus monkeys (Fig. 2) ranging in the study grid of the Tai Monkey Project (McGraw et al., 2007). Groups of these monkeys are fully habituated and have been under nearly continuous observation since 1990. Data reported were collected between July 2010 and February 2014. In contrast to those collected on *Cercocebus atys* at Tai (McGraw et al., 2011), the data reported here were not collected continuously over the sampling period. There were several intervals during the observation period when sampling was interrupted due to security issues arising from political unrest in Cote d'Ivoire. These issues forced us to suspend data collection for several months at a time, though field assistants remained at our research station. Due to the unevenness of the sampling, we emphasize that the dietary data reported here do not reflect the full breadth of what each species consumed between 2010 and 2014. For example, our feeding profiles contain fewer overall plants and fewer fruits than the dietary profiles of *C. polykomos* and *P. badius* presented by Korstjens (2001) and Korstjens and colleagues (2007). We recognize this as a limitation, but emphasize that the diet profiles presented are useful because they are accompanied by corresponding processing profiles.

We used focal animal sampling to record the diet and oral processing frequencies of adult males and females during five minute focal periods. The distance between observer and focal animals ranged from 3 to 30 meters and we typically used binoculars to observe subjects feeding at distances greater than 10 meters. If contact with the focal animal was lost before the five minute period had elapsed, we did not use data from that sampling interval. During each focal period, we recorded the number of times the focal animal introduced a food item into its oral cavity and labeled each of these behaviors an action. For each action, we recorded the plant

species, the plant part ingested (e.g., fruit, leaf, seed, flower, bud, etc.), and whether the item was young or mature, if discernable. We did not attempt to identify species of animal matter consumed.

We recorded the manner and frequency in which a monkey used different portions of its dentition to ingest (incise) and/or masticate (chew) each food item. In contrast to sooty mangabeys (McGraw et al., 2011) or Tana River mangabeys (Wieczkowski, 2014), colobus monkeys at Tai do not exhibit a great diversity of oral processing behaviors and we only recorded the number of times the incisors were employed (incision) and the number of masticatory (chewing) cycles. Thus, oral processing refers to the totality of ingestive and masticatory events. It was difficult to discern when the canines were used in an isolated fashion or even in combination with the incisors, so we did not attempt to score canine use. It is therefore possible that some observations of incision include use of the canines. During most feeding bouts, monkeys introduced foods to the mouth with their hand and either used the incisors to disengage the food from the substrate, as in biting a leaf off a twig or, if the food had already been separated from its substrate (e.g., handful of leaves stripped from a branch), directed the food toward the tooth row in the back of the mouth. In other instances, the incisors were used in combination with the lips and tongue to pluck small foods from twigs as in the procurement of *Dialium aubrevillei* fruits. In such cases, a monkey would typically introduce at least one fruit into the oral cavity for every action. Other food items required significantly more incisal preparation, as with *Pentaclethra macrophylla* consumption. In these cases, processing involves considerable incisal work because the seeds are housed within a tough woody pod. Pieces of the incised pods could be eaten or discarded. We did not attempt to quantify how much of a pod was consumed and recorded only the number of times the incisors were used in a gnawing fashion. Some authors recognize multiple kinds of incisal preparation using terms such as bites, picks, scrapes, or nips (e.g., Ungar, 1994; Yamashita, 2003); however, due to observational limitations, we were not sufficiently confident that subdividing this category could be consistently applied. Therefore, we made no distinction in the use of incisors. Thus, each

time the incisors were used in any fashion and regardless of the presumed forces involved, we scored the behavior as a single incisive event. Using this protocol, we calculated the average number of incisions and the average number of masticatory (chewing) cycles per action and per food for each species. WSM collected the first month of ingestive behavior data and during this period instructed two field assistants in the sampling protocol. Inter-observer reliability was checked on four occasions using the method described by Caro et al. (1979), which involves comparing processing frequencies scored by multiple individuals over a designated sampling period. We achieved a high level of inter-observer reliability during each sampled test and in no case did comparative tests yield differences greater than 2%.

We performed a materials property analysis of *Pentaclethra macrophylla* using a portable FLS-I tester (Lucas Scientific) specifically designed for use in the field. The machine consists of a ball-screw hand-cranked crosshead drive. Vertical displacements of the crosshead are monitored by a linear variable differential transformer (LVDT) and resultant forces are recorded using a load cell. The unit is powered by an interfacing computer which collects and analyses the data resulting in accurate estimations of food material properties.

Seed pod and seed flesh toughness

To measure seed pod toughness R , samples were cut from seed pods collected from the forest floor. Efforts were made to sample only fresh pods: those that appeared to have fallen or been dropped recently from trees, that did not appear old, were not buried under the detritus of the forest floor, and showed no overt signs of degradation. We are not able to say definitively that the pods we tested were completely unaffected by being on the forest floor even for short periods of time; however, given that the pods themselves are not moisture laden and are somewhat lignified, they are not prone to rapid degeneration. Further, seeds contained within pods are protected from the outer environment and should slow degeneration of the material. This point is supported by the mechanical properties values we obtained (see below) that are

close to typical fruit values in the literature. Toughness tests were performed in a longitudinal direction to simulate the course in which a crack would propagate when being eaten by *C. polykomos*, who appears to rip apart the pod along the grain (Fig. 3). Seed pods were split along the seam and a cuboid section was cut for toughness testing (Fig. 4a). We did not perform tests across the grain of the pod. While it is true that some of the monkey's processing effort must have gone into cutting across fibers, we hypothesize that the majority of effort is directed to splitting the pod longitudinally. Our reasoning is based on the way the fibers are arranged along the longitudinal axis: materials with this arrangement (e.g., wood) generally show high anisotropy in their mechanical properties, so cutting across the grain requires considerably more energy than cutting along fibers. With this in mind, it would energetically be most efficient for monkeys to initiate a crack and propagate it longitudinally to access the seeds within, since cutting across the grain would require considerably more effort. We believe it is clear from the shape of the access hole produced (Fig. 3) that the majority of work is done in this longitudinal direction and sampled pods accordingly. Seeds were removed from pods and the seed coat removed from the seeds. The seed flesh was then cut into cuboid sections for toughness testing. There was no obvious grain to the seeds, so they were not tested in any particular direction.

Being bulk food items, both seed pod and seed flesh toughness was measured using the wedge test (Fig. 4b). This test propagates a controlled crack through the material being tested. A sharp wedge of 15° was driven through the seed pod and the resultant force was measured using a load cell with the depth of the fracture given by the wedge displacement. The work done in cutting the sample is given by the area under the force-displacement curve; however, the work done is not solely fracture resistance, but also comprises elastic deformation not used in fracture, friction, and adhesion. These three factors combined must be excluded in order to derive an accurate measure of the work of fracture. They were estimated by performing a second pass where the wedge was driven through the same displacement as the actual test (the first pass) into the already-cut tissue. The work done in the second pass was deducted from that done in the

actual test. Dividing this quantity by the area of cut gave an estimate of R (Lucas, 2004a; Lucas et al., 2011; Ennos, 2012).

Pod hardness and reduced elastic modulus

The hardness and reduced elastic modulus of the seed pod were measured using a sharp indent test. Samples were cut and prepared so as to give a flat surface (Fig. 5). In this test a tungsten carbide Vickers pyramid was pressed into the seed pod for a distance of around 1mm and then removed (Fig. 6a), while the resultant force and displacements were measured (Fig. 6b). Hardness was calculated using equation 1 where F_{max} is the force that causes a permanent deformation of a material and A_p is the area of contact projected on to the specimen surface, which can be estimated from indenter geometry.

$$H = F_{max} / A_p \quad (1)$$

The reduced elastic modulus E_r can be calculated by using equation 2 (Oliver and Pharr, 1992). Where β is a function of indenter shape, set at $\beta = 1.153$, and S is the slope immediately after unloading (the steepest part of the unloading slope), i.e., after F_{max} has been reached (Fig. 4b).

$$E_r = 2 \beta^{1/2} A_p^{1/2} S \quad (2)$$

Fruit modulus

Fruit modulus was measured using a blunt indent test. This method takes advantage of advances in the field of indentation, especially the introduction of spherical indenters that allow the calculation of the modulus of soft materials such as fruit flesh. The test is described in detail

within this issue by Van Casteren et al. (submitted). Samples require very little preparation as just a flat surface is necessary for indentation with a hemispherical probe. The test follows a format of load and then relaxation; this requires the application of a steadily-increasing load to the sample for 10 seconds. The displacement is then held and the load allowed to ‘relax’ for a further 90 seconds. Mechanical analysis assumed a multi-term exponential decay of the load, with a best-fit curve defined as that which minimized the correlation coefficients between each of the constants. Two terms were deemed sufficient to characterize the relaxation curve. This allowed calculation of instantaneous (E_0) and infinite (E) moduli. These two terms can be considered the upper and lower bounds of the elastic modulus of the material being tested. E_0 is the value that can be expected for the material loaded instantaneously, whilst the E represents a fully relaxed modulus and is an estimation of the elastic behavior of a material over an infinitely slow loading regime.

Deriving fracture toughness K_c

Using our values for toughness and modulus in the seed pod and seed flesh it is possible to derive K_c , the critical stress intensity factor needed to cause a fracture (also referred to as fracture toughness) using equation 3. The term K_c has the units $\text{MPa m}^{0.5}$, therefore, the intensity of the stress depends on the square root of crack length. This term allows us to demonstrate the effect a crack of a given unit length will have on the intensity of stress in the loaded material (Lucas, 2004a).

$$K_c^2 = ER \quad (3)$$

All research was carried out under OSU Animal Use Protocol # 2008A0051-R2 and followed institutional and governmental regulations for the ethical treatment of subjects.

Results

During our observations red colobus consumed 32 plants identifiable to species (Table 1). Approximately three quarters of the red colobus diet consisted of leaves, the majority of which we described as immature. The two most frequently consumed foods by red colobus were young leaves of *Caloncoba brevipes* (12.6%) and *Strephonema pseudocola* (12.5%). The diet of black and white colobus was considerably less diverse; these monkeys consumed 10 plants that could be identified to species (Table 2). Black and white colobus consumed fewer (< 50%) leaves than red colobus; however, a greater proportion of these were mature leaves. The most frequently consumed foods by black and white colobus were *Pentaclethra macrophylla* fruits (pods and seeds; 26.6%) and the mature leaves of *Diospyros canaliculata* (26.4%).

Table 1 reports mean incisions and mean mastication (chewing cycles) values for each plant part consumed by red colobus, and Table 2 reports these values for the 10 plants consumed by black and white colobus monkeys. When all foods are considered, red colobus incise an average of 1.68 times per ingestive event whereas black and white colobus incise an average of 3.09 times per ingestive event. Mean incisions (specific to parts of plant species) range between 0.15 and 3 for red colobus and between 0 and 27.7 for black and white colobus. Incision means for 21 of the 23 plant parts (from 13 plant species) ingested by black and white colobus fell at or below 3. Values for two foods are extreme outliers: fruits of *Pentaclethra macrophylla* required an average of 27.7 incisions per action and fruits of *Calpocalyx brevibracteatus* required an average of 22 incisions per action. Fruits from both of these leguminous trees are housed in long, woody pods and their processing is discussed below. Figure 7 displays results of the bootstrap resampling procedure that was performed with and without *Pentaclethra macrophylla* feeding data. This was done because we were interested in determining how much of the incisive work performed by *C. polykomos* was attributed to *P. macrophylla* consumption. Note that we did not exclude *Calpocalyx brevibracteatus* processing in the bootstrap calculations because this food comprises such a small percentage of the sampled diet; however, we note that

including it would result in an even greater disparity in incision means. Results of the analysis reveal that the 99% confidence intervals do not overlap for any sample. That is, when all foods are considered, black and white colobus incise their foods more frequently than do red colobus; however, when *Pentaclethra macrophylla* is excluded from the analysis, red colobus incise their food more frequently than do black and white colobus. In other words, processing of *Pentaclethra macrophylla* accounts for the large difference in incisive processing between the two colobus.

When all foods are considered, red colobus masticated an average of 17.5 times per ingestive event (Table 1). Black and white colobus chewed their food more often, averaging 20.4 chewing cycles per ingestive event (Table 2). Figure 8 reports results from the bootstrap analysis which indicates that black and white colobus chew significantly more often than do red colobus monkeys, a result that holds regardless of whether *Pentaclethra macrophylla* consumption is considered or not. Among red colobus, mean masticatory cycles range between 9 (consumption of young *Macaranga heterophylla* leaves) to 27.3 (consumption of unripe *Diospyros sanza-minika* fruit) per action. Mean masticatory cycles for black and white colobus range between 7.2 (consumption of *Diospyros canaliculata* buds) to 31 (consumption of mature leaves from unidentified lianes).

Analysis of Pentaclethra macrophylla pod and seed

In addition to its large contribution to the diet of black and white colobus, *Pentaclethra macrophylla* is responsible for the major difference in processing behavior between colobine species. We therefore undertook a material property analysis of both the pod and seed. The *P. macrophylla* seed pod appears rather fibrous with the fibers arranged in a longitudinal direction (Fig. 3). There also appears to be a layered arrangement to the pod with fibers being on top of a more homogeneous matrix below (Fig. 5). This pod forms an obvious form of protection to the

consumable seeds that lie within. Toughness was very high for the seed pod (mean of $10603.32 \pm 5148.85 \text{ J m}^{-2}$). This figure relates quite well to those of some other hard legume pods: *Intsia palembanica*, for example, has a work to fracture of 6950 J/m^2 along the pod length (Lucas, 2004). The pod toughness was two orders of magnitude higher than that of both the seed coat and the fruit flesh, which were very similar at 411.65 ± 109.15 and $400.43 \pm 179.04 \text{ J m}^{-2}$, respectively, and well within the range one would expect for fruit (Vogel et al., 2008; Constantino et al., 2009). A one-way ANOVA and Tukey Post Hoc test (Fig. 9) demonstrated that the toughness of the seed pod was significantly higher than that of the seed coat and flesh, which were not significantly different from each other ($F_{2,27} = 39.16, p < 0.001$).

The reduced elastic modulus measured by sharp indentation of the seed pod averaged $215 \pm 29.0 \text{ MPa}$, which is considerably lower than materials like medium-density wood, e.g., 4000 MPa (Ennos, 2012) or macadamia nut shells, e.g., 6200 MPa (Wang and Mai, 1994), but far higher than the range of fruit, e.g., $1\text{--}5 \text{ MPa}$ (Constantino et al., 2009). A one-way ANOVA and Tukey post hoc test (Fig. 10) demonstrated that pod E_r was significantly higher than our measurements of seed flesh modulus that has a mean upper and lower bound of 2.08 ± 1.76 to $2.82 \pm 2.32 \text{ MPa}$. These measures of seed flesh modulus did not significantly differ from each other ($F_{2,23} = 563.6, p < 0.001$).

The seed pod hardness is $9.73 \pm 3.41 \text{ MPa}$, which is well below the range of enamel ($2000\text{--}5000 \text{ MPa}$), meaning the pod material should not cause any immediate wear (removal of material) though it may rub the enamel surface (move the material around). It is also well below values for dentine ($\sim 60 \text{ MPa}$), so the same applies to contacts with that tissue. Table 3 compares the material properties of the seed pod and fruit flesh to those obtained for generalized primate foods and other ecologically relevant materials such as wood. We also report the derived K_c values for *P. macrophylla* seed flesh (upper bound = $0.033 \text{ MPa m}^{0.5}$, lower bound $0.028 \text{ MPa m}^{0.5}$) and seed pod ($1.51 \text{ MPa m}^{0.5}$). The fruit flesh of *P. macrophylla* is within the range of generally accepted values for fruits eaten by primates (Vogel et al., 2008; Constantino et al.,

2009). The seed pods have a modulus in the range of bark ($\sim 10\text{--}600$ MPa; Constantino et al. [2009]) but a much larger toughness in a longitudinal direction making the seed pod a rather ductile and tough material. Although the seed pods appear woody in texture, they have a modulus an order of magnitude lower than a medium density wood and a toughness of around one third of this generalized figure.

Discussion

Our purpose for quantifying the basic oral processing behaviors of two Tai colobines is based on the assumption that attempts to interpret primate dentognathic morphology using gross dietary categories alone are inadequate (Ross et al., 2012). Inventories highlighting the breadth of a primate's ingestive and oral processing behaviors can provide an additional source of information; however, ethograms lacking data on the frequencies behaviors are performed may also fall short of elucidating those pressures most responsible for shaping the tissues involved in food ingestion and reduction. We contend that to more fully understand the selective forces routinely operating on the primate feeding apparatus, it is necessary to combine information on food material properties with that on the frequencies that common and rare behaviors are employed. Obtaining actual chewing counts in natural contexts is critical since it appears that the relationship between processing frequencies and time spent feeding is not constant, meaning that it is not possible to derive the number of chewing cycles from feeding bout length. Wright et al. (2008) quantified chewing rates in several species of captive Asian colobines and, holding food material property constant (in this case, leaf toughness), demonstrated that while two leaf monkey species did not differ in length of time spent chewing, they did differ in chewing speed. Indeed, *Trachypithecus* spp. chewed its food twice as fast as *Pygathrix* spp. Mastication number was not recorded by Wright and colleagues (2008); however, the difference in rate implies a difference in the number of chewing cycles between study taxa, a result consistent with data presented in this study. The message here is that because the work performed during mastication over a given interval may vary due to differences in chewing speed, there is value in tabulating

the number of times primates perform food processing behaviors. This logic has long formed the basis for field studies of positional behavior designed to facilitate interpretations of the primate locomotor skeleton (e.g., Fleagle, 1976).

Red colobus and black and white colobus at Tai have diets that are accompanied by distinctive oral processing regimes. Over the course of the sampling period, red colobus were more folivorous than black and white colobus, with the former consuming over 75% leaves and buds compared to approximately 47% leaves and buds in *C. polykomos*. Based on percent folivory alone, it is not unreasonable to predict that red colobus would—on average—generate more chewing cycles than black and white colobus in response to a diet comprised of foods (leaves) that, on average, tend to be tougher than most fruit (Dominy et al., 2001; Lucas, 2004b). Our field observations show this not to be the case: black and white colobus generate more masticatory cycles across the breadth of their sampled diet than do red colobus. One explanation is that Tai red colobus target young leaves, whereas black and white colobus consume greater quantities of mature leaves. Indeed, our data reveal that *C. polykomos* at Tai consumed nearly three times as many (30%) mature leaves as did *P. badius* (10.1%). We have not yet collected toughness data on leaves consumed by Tai colobines; however, there are considerable data that indicate an association between leaf maturity and toughness (e.g., Hill and Lucas, 1996; Lucas et al., 2000; Yamashita, 2003; Yamashita et al., 2009). If this relationship holds at Tai and it is determined that mature leaves consumed are tougher than young ones, then the greater chewing frequencies performed by *C. polykomos* could be attributed to a tougher diet as opposed to one that is simply more folivorous (since in this case, it is not). This hypothesis is weakened by the fact that for several tree species, there was no difference in the number of chewing cycles used to process mature versus young leaves and in the case of one food (*Guibourtia ehie*), red colobus chewed young leaves slightly more than they did their mature counterparts. It is not clear if this result is an artifact of small sample size (e.g., *Guibourtia ehie* leaves comprise less than 1% of the total red colobus diet); however, the lesson here is that material property data on all consumed foods are required before we can make reliable interpretations of processing regimes.

Black and white colobus at Tai employ their anterior dentition more frequently and, we suspect, more aggressively during food ingestion (i.e., incision) than do red colobus. Our field observations confirm that the difference in incision frequencies is attributable to *C. polykomos*' consumption of pods and seeds from a single tree: *Pentaclethra macrophylla*. The significance of *P. macrophylla* to the behavioral-ecology of *C. polykomos* is well-documented and the procurement and processing of its fruit is known to influence, among other things, activity patterns, ranging behavior, and postural behavior of populations at two localities (Dasilva, 1992, 1994; McGraw, 1998; Korstjens, 2001). The processing of *P. macrophylla* pods is a time and labor intensive activity, and it is not uncommon for black and white colobus to spend 15 minutes orally processing a pod in order to access the seeds within. During such bouts, *C. polykomos* typically adopt seated postures in secure perches, grasp a single pod with both hands, and gnaw the pod in manner similar to way we eat an ear of corn. We suspect that considerable incisive forces are involved, as evidenced by the fact that the heads of monkeys will occasionally snap sharply backwards once an animal has separated a piece from the pod or, alternatively, if it loses its incisal grip. The pod is manipulated manually and monkeys will frequently twist and rotate the pod—even as it is being gripped by the incisors—presumably to loosen pod fibers. During some feeding bouts, much of the pod is ingested whereas during other bouts, fibrous strips are torn from the pod and spit out and only the seeds are consumed. We did not collect systematic data on processing duration; however, we are confident that this food requires the longest handling time of any item and that its ingestion requires the greatest work.

What makes ingestion and reduction of this food so challenging, and could a reliance on this or some materially similar food in the *C. polykomos* diet explain features of its dentognathic complex? The material analysis reveals that *P. macrophylla* has a pod made of tissue with high work of fracture and moderately low stiffness, which would make it difficult to process. The high work of fracture seems related to the longitudinally arranged fibers and layered nature of the pod structure (Fig. 3), although further investigation of how the material in the pod is

arranged is needed to confirm this. While a moderately low stiffness may seem counterproductive for a protective seed coat, its compliance may make it even more difficult to fracture. As a crack propagates, movement in the material may aid to dull the crack tip, requiring more energy to fracture the material further. The combination of both high toughness and low modulus would mean that considerable energy would need to be imparted into the material to initiate and encourage fracture. Brittle catastrophic failure like that seen in nut and seed shells due to the high modulus of a material is unlikely to happen, meaning that *C. polykomos* would have to ensure continued manipulation with its teeth to remove the material and access the seeds within. Our field observations of prolonged and aggressive feeding bouts strongly support this hypothesis.

The low modulus of the seed pod may arise from a degree of void space in the pod material, possibly due to its fibrous layered structure. There are probably a lot of voids in these pods that will lower the resistance of the material to sharp indentation, the indenter tip separating the fibers that are present. This may be relevant to this particular study as the tips of *C. polykomos* teeth may act in a similar fashion when pressed into the material during the processing of the seed. Additional testing is required to confirm this. *C. polykomos* may be able to take advantage of the low hardness of the seed pod material as pressure imparted by the teeth should easily permanently deform the material. These deformations could then be taken advantage of using the teeth to force and extend crack propagation and allow the eventual breakdown of the pod with teeth to access seeds within.

It therefore appears that although the pods and seeds of *P. macrophylla* are not especially hard, pod toughness, pod geometry, and the spacing and orientation of the pod's fibers pose significant processing challenges to black and white colobus. We assume, but cannot yet demonstrate, the frequent and aggressive incisive behaviors employed by *C. polykomos* to breach the seed pod involves particularly high loads which are translated from the chewing muscles, through bone and teeth, to the pods. Has reliance on this—or some materially similar food—

been responsible for shaping the masticatory morphology of black and white colobus? Evidence exists that this might be the case. There have been numerous attempts to interpret variation in the cranio-dental morphology of African colobines (Shultz, 1958, O'Higgins and Pan, 2004, Cardini and Elton, 2009) and several of these have alluded to feeding differences, including tendencies toward seed-eating, as being selectively important. Verheyen (1962) and later Hull (1979) observed that the portions of the crania that best distinguished species of black and white colobus from each other were portions of the face and palate, leading these authors to postulate that feeding differences were especially important during *Colobus* speciation. Further—and consistent with the notion that black and white colobus are not obligate folivores (Oates et al., 1996)—Hayes and colleagues (1996) argued that the reduced canine dimorphism in *C. polykomos* was related to the demands of processing seeds: “In processing a variety of seeds in the diet, teeth may fracture and fragment both rigid, brittle structures, such as hard seed coverings, and tough pliant substances, such as seed storage tissues, both of which may generate large stresses on the teeth during mastication (736).” We cannot determine how long black and white colobus have consumed woody plants and seeds; however, it has been argued that seed-eating is primitive for colobines and that the colobine bilophont molars “make as much sense for processing seeds as they do for processing leaves” (Lucas and Teaford, 1994:203). Based on their analysis of colobine dentition, Lucas and Teaford (1994) argued that the ancestral colobines were likely adapted to a granivorous diet and that the seeds ingested by them were likely to be pliant and tough. We concur with this hypothesis and contend that in the case of *Colobus polykomos* at Tai and elsewhere in West Africa (Dasilva, 1992, 1994), the consumption of *Pentaclethra macrophylla* pods and seeds is a diagnostic feature of this monkeys' diet and that the associated processing behaviors are strikingly different from those observed in sympatric red colobus monkeys. Given these behavioral data, and the multiple studies suggesting that dental and cranial differences among black and white, red, and olive colobus are attributable to aspects of diet generally and seed/seed pod consumption specifically, it is not unreasonable to

hypothesize that a specialization on seeds and their woody pods may have facilitated the divergence of African colobines in the late Miocene (Ting 2008).

Conclusions

Despite the centrality of diet to primate studies, descriptions of the range of ingestive and processing behaviors used by most primates are not yet available and those that exist tend to be derived from primates with extreme diets or behaviors such as exudate feeders or granivores (cf. Milton, 1978; Iwano and Iwakawa, 1988; Corlett and Lucas, 1990; Kinzey and Norconk, 1990; Ungar, 1990, 1994; Yamashita, 2003). Rarer still are data providing frequencies with which primates utilize even routine behaviors in their processing inventories and some of the most fundamental food processing questions—e.g., How frequently does a primate chew its food?—are unanswerable for most taxa. The paucity of data makes comparisons difficult and we are reluctant to extrapolate conclusions beyond reasonable boundaries of our data; however, we can compare our findings to those of another cercopithecoid at Tai—the sooty mangabey *Cercocebus atys*—that was studied with identical methods (McGraw et al., 2011). The differences in processing behaviors between the three Tai cercopithecoids are striking: although black and white colobus employed its incisors (3.09 incisions per action) significantly more often than did the red colobus (1.68 incisions per action), values for both colobines fall below those reported for sooty mangabeys (4.4 incisions per action). In terms of mean number of chewing cycles, those reported for red colobus (17.49 mastications per action) and black and white colobus (20.4 mastications per action) are much greater than those reported for sooty mangabeys (7.12 mastications per action). Of course, these results must be interpreted in view of the fact that sooty mangabeys have cheek pouches, raising the possibility that additional masticatory and/or incisive processing occurred after the focal period ended. Nevertheless, if this additional processing did not yield significant changes in ingestive and/or processing frequencies, then the message from this study is that the colobines chew much more than do sooty mangabeys, but that the latter cercopithecine employs their incisors more frequently than either colobine. This result

is especially surprising given the black and white colobus' heavy reliance on *Pentaclethra macrophylla* pods and seeds which require such high frequencies of incision.

Can differences in the masticatory morphology of these colobines be attributed to differences in diet and/or food processing? Daegling and McGraw's (1991) study of comparative mandibular morphology of *P. badius* and *C. polykomos* noted an apparent incoherence between biomechanical performance measures and the mechanical demands of the species' respective diets; specifically, the red colobus appeared to have relatively stronger jaws while exploiting a less challenging diet than the king colobus. In that study, the demands of feeding on *Pentaclethra* emphasized dietary hardness and masticatory (as opposed to ingestive) forces. The present work sheds additional light on this apparent paradox. What is clearer now is that the seeds of *Pentaclethra* pose no particular mechanical challenges, but it is the work required accessing these seeds that entails greater effort for the black and white colobus. It is in hindsight noteworthy that the one performance measure in *C. polykomos* that clearly exceeded that in *P. badius* was parasagittal bending resistance. One context in which this load would be particularly important would be in the use of the incisors to broach the tough pods of *Pentaclethra*. Even so, the jaws of *P. badius*—interpreted in the context of strict covariance of feeding mechanics and mandibular form—still suggest adaptation to a particularly demanding diet for which there remains little convincing evidence. Thus, while our data reveal co-occurrence of seed-eating and ingestive work, this observation is far from adequate for implicating a causal connection. Nevertheless, by integrating oral processing data from the field with those on material properties across the entirety of the diet (e.g., Vogel et al., 2014), we establish the context for studies—such as those on bone stiffness (e.g., Daegling et al., 2011a, b) and secondary remodeling (Bouvier and Hylander, 1996; Lad et al., 2013)—that help decipher how load frequency and load magnitude influence the structural and material variation in masticatory morphology.

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Figure legends

Figure 1 The Western red colobus, *Piliocolobus badius*, in the Ivory Coast's Tai Forest.

Figure 2 The Western black and white or King colobus, *Colobus polykomos*, in the Ivory Coast's Tai Forest.

Figure 3 An example of the seed pod of *Pentaclethra macrophylla* that has been orally processed by *C. polykomos*. White lines indicate a typical sample location. S indicates the positioning of the consumed seeds.

Figure 4 A) A sample prepared before testing. The pod is split along its seams and a sample cut from one side. The arrow indicates the direction of the test that ran along the longitudinal axis of the seed pod. B) A schematic of the wedge test used to measure material toughness. A wedge is driven through a material propagating a crack, the force (F) required to do so is measured by a force transducer. The length of the crack is measured by the wedge displacement (D) and the area of the crack is calculated from this displacement and sample width (W).

Figure 5 A cross sectional view of the seed pod of *P. macrophylla* showing the fibrous and layered nature of the material that makes up the outer casing.

Figure 6 A) A schematic drawing of a sharp indent hardness test. A tungsten carbide Vickers indenter (V) is pushed into a flat sample using a force (F) for about a millimeter and then removed. B) During this process the force and displacement is recorded allowing the calculation of hardness and reduced elastic modulus. Figure redrawn from Lucas (2004).

Figure 7 Results of bootstrap analysis of incision frequencies per ingestive event (actions) for red colobus (top, $N = 3,882$), black and white colobus with all foods considered (middle, $N = 5,167$), and black and white colobus minus feeding on *Pentaclethra macrophylla* (bottom, $N = 4,740$). Means were calculated from resampling with replacement at original sample sizes over 10,000 iterations; the histograms represent the frequency distribution of these resampled means. In each case, 99.9% confidence intervals do not include the observed mean values for the other cases, strongly suggesting that when all foods are considered, black and white colobus incise their food more frequently than do red colobus monkeys. That this difference disappears when consumption of *Pentaclethra macrophylla* is omitted suggests that this difference in oral processing behavior is due to the consumption of a single food.

Figure 8 Results of bootstrap analysis of mastication frequencies (chewing cycles) per ingestive event for red colobus (top, $N = 3,882$), black and white colobus with all foods considered (middle, $N = 5,167$), and minus feeding on *Pentaclethra macrophylla* (bottom, $N = 4,740$). Means were calculated from resampling with replacement at original sample sizes over 10,000 iterations; the histograms represent the frequency distribution of these resampled means. Bootstrapped 99.9% confidence intervals are non-overlapping in both cases, indicating that black and white colobus chew significantly more often than do red colobus monkeys. This result holds regardless of whether *Pentaclethra macrophylla* is considered or not.

Figure 9 Box plots showing the recorded toughness (J m^{-2}) for *P. macrophylla* A) seed pod and B) seed coat and seed flesh. A one way ANOVA and Tukey post hoc test demonstrated that the pod had significantly higher toughness than the seed skin and flesh, which were not significantly different from each other ($F_{2,27} = 39.16, p < 0.001$).

Figure 10 Box plots showing the A) reduced elastic modulus (E_r) of seed pod and B) the instantaneous E_0 and infinite E of the seed flesh of *P. macrophylla*. A one way ANOVA and Tukey post hoc test demonstrated that the pod had significantly higher modulus than the seed skin and flesh, which were not significantly different from each other ($F_{2,23} = 563.6, p < 0.001$).

Figure 11 *Colobus polykomos* feeding on *Pentaclethra macrophylla*. The brown pods, which are approximately 12 inches in length when mature, can be seen suspended from multiple branches.

Table 1. Average incision and mastication values per ingestive action for plants consumed by *Piliocolobus badius* during sampling period^a

Plant species and part	Mean incision per action	Mean mastication per action	% Contribution to diet
<i>Anthonota sassandraensis</i>			
Fruit	1.07	20.61	3.1
Young leaf	1.75	25.00	0.2
<i>Berlinia grandiflora</i>			
Bud	1.20	12.20	0.3
Young leaf	1.20	14.20	0.3
<i>Bussea occidentalis</i>			
Young leaf	2.80	16.30	0.6
<i>Caloncoba brevipes</i>			
Young leaf	0.15	20.80	12.6
<i>Calpocalyx brevibracteatus</i>			
Unripe fruit	2.90	14.80	0.2
Mature leaf	2.20	20.90	1.3
Young leaf	1.90	14.00	1.4
<i>Carapa procera</i>			
Young leaf	1.60	12.40	1.2
<i>Combretum aphanopetalum</i>			
Young leaf	1.30	12.90	0.8
<i>Coula edulis</i>			
Bud	1.60	17.70	0.6
Unripe fruit	1.20	13.80	2.1
Mature leaf	1.30	18.40	0.9
Young leaf	1.30	19.30	5.8
<i>Dialium aubrevillei</i>			
Unripe fruit	1.40	15.10	0.7
Ripe fruit	1.30	13.30	0.5
<i>Diospyros sanza-minika</i>			
Unripe fruit	3.00	27.30	2.5
<i>Drypetes gilgiana</i>			

Mature leaf	1.50	10.50	2.5
<i>Erythrophleum ivorense</i>			
Young leaf	2.40	18.90	0.6
<i>Garcinia afzelii</i>			
Young leaf	1.50	13.90	1.5
<i>Gilbertiodendron preussi</i>			
Bud	2.20	11.20	1.7
Young leaf	2.10	15.70	5.6
<i>Guibourtia ehie</i>			
Unripe fruit	1.30	17.80	0.4
Mature leaf	1.10	13.90	0.2
Young leaf	0.40	15.50	0.6
<i>Heritiera utilis</i>			
Young leaf	1.10	13.10	1.7
<i>Irvingia gabonensis</i>			
Bud	1.00	10.40	0.8
Young leaf	1.60	12.80	0.6
Liane (unknown sp.)			
Young leaf	1.50	16.40	0.4
<i>Macaranga barteri</i>			
Young leaf	1.20	12.70	0.2
<i>Macaranga heterophylla</i>			
Young leaf	1.00	9.00	0.8
<i>Memecylon lateriflorum</i>			
Unripe fruit	2.10	18.90	0.8
<i>Nauclea pobeguinii</i>			
Young leaf	2.50	14.70	1.4
<i>Parinari aubrevillei</i>			
Young leaf	1.00	14.10	0.2
<i>Parkia bicolor</i>			
Unripe fruit	2.90	18.40	1.8
Young leaf	1.70	14.60	0.4

<i>Pentaclethra macrophylla</i>			
Mature leaf	2.60	14.00	1.9
<i>Pentadesma butyracea</i>			
Blossom	1.10	19.10	0.6
Bud	2.00	20.00	0.2
Unripe fruit	1.10	15.50	0.2
Mature leaf	1.40	23.00	3.3
Young leaf	2.30	14.70	0.2
<i>Piptadeniastrum africanum</i>			
Unripe fruit	1.00	8.20	0.4
<i>Scotellia chevalieri</i>			
Young leaf	1.50	13.80	0.4
<i>Scytropetalum tieghemii</i>			
Blossom	1.90	11.40	0.4
Bud	1.90	11.80	2.1
Fruit	1.00	5.00	0.2
Young leaf	1.50	12.70	2.8
<i>Strephonema pseudocala</i>			
Bud	2.30	16.60	0.4
Unripe fruit	1.40	25.00	0.8
Young leaf	1.80	17.20	12.5
<i>Trichoscypha arborea</i>			
Unripe fruit	3.00	15.60	0.4
Young leaf	1.40	13.40	0.7
<i>Uapaca esculenta</i>			
Young leaf	1.40	15.60	0.9
<i>Xylopia parviflora</i>			
Young leaf	2.50	15.80	4.8
Unidentified			9.5
Grand	1.68	17.49	
N Scans			518
N Actions			3,886

^a Oral processing behaviors are broken down by plant part and the contribution of each part to the total diet during field observations is reported.

Table 2. Average incision and mastication values per ingestive action for plants consumed by *Colobus polykomos* during sampling period^a

Plant species and part	Mean incision per action	Mean mastication per action	% Contribution to diet
<i>Baphia bancoensis</i>			
Mature leaf	0.00	17.4	0.45
Young leaf	0.00	16.9	0.45
<i>Bussea occidentalis</i>			
Fruit	21.10	14.8	12.30
Mature Leaf	1.00	23.7	0.20
<i>Calpocalyx brevibracteatus</i>			
Fruit	22.00	13.0	2.80
Unripe fruit	8.40	11.3	0.40
<i>Diospyros canaliculata</i>			
Bud	1.00	7.2	0.20
Unripe fruit	1.00	21.1	1.90
Mature leaf	0.30	26.7	26.40
Young leaf	0.90	19.3	9.01
Liane (unknown spp.)			
Leaves	0.00	31.0	0.21
<i>Masularia accuminata</i>			
Mature leaf	1.00	13.7	0.40
<i>Pentaclethra macrophylla</i>			
Fruit	27.70	24.4	26.60
Mature leaf		21.3	0.20
<i>Peperomia guinense</i>			
Fruit	0.00	12.5	4.30
<i>Polyalthia oliveri</i>			
Mature leaf	0.90	11.5	0.86
Young leaf	0.10	11.9	3.40
<i>Samanea dinklagei</i>			
Fruit	1.00	26.2	1.30
<i>Vitex micranthra</i>			

Mature leaf	0.24	14.3	0.95
Young leaf	0.25	11.2	4.30
Unidentified			3.37
Grand	3.09	20.4	
N Scans			469
N Actions			5,167

^a Oral processing behaviors are broken down by plant part and the contribution of each part to the total diet during field observations is reported.

Table 3. Placing the experimental recorded moduli and toughness in combination with derived fracture toughness (K_{c}) of *P. macrophylla* with generalized values for broad groups of primate foods and other ecologically relevant materials

Tissue	Modulus	Toughness	K_{c}	Reference
	(Mpa)	(J m ⁻²)	(MPa m ^{0.5})	
Fruit	2.50	500.00	0.030	Constantino et al. (2009)
Fruit flesh (<i>P. macrophylla</i>)	2.80 (E_i)	400.00	0.033	This study
	2.10 (E_{∞})		0.028	
<i>Tamarindus indica</i> fruit (ripe)	418.27	3371.97	1.187	Yamashita et al. (2012)
<i>Tamarindus indica</i> fruit (unripe)	3.87	1397.54	0.074	Yamashita et al. (2012)
Leaf Lamina	50.00	250.00	0.100	Lucas (2004), Ang et al. (2007)
				Constantino et al. (2009)
Bark	500.00	2000.00	1.000	Vogel et al. (2008), Constantino et al. (2009)
Seed pod (<i>P. macrophylla</i>)	215.70	10603.00	1.510	This study
Seed shell	5000.00	1500.00	2.730	Constantino et al. (2009)
Wood	4000.00	30000.00	10.950	Ennos (2012)

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11