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Fallback Foraging as a Way of Life: Using Dietary Toughness to Compare the Fallback Signal Among Capuchins and Implications For Interpreting Morphological Variation

Barth W. Wright,[1]* Kristin A. Wright,[1] Janine Chalk,[2] Michele P. Verderane,[3]
Dorothy Fragaszy,[4] Elisabetta Visalberghi,[5] Patricia Izar,[3] Eduardo B. Ottoni,[3]
Paul Constantino,[6] and Christopher Vinyard[7]

[1]*Kansas City University of Medicine and Biosciences, Kansas City, MO*
[2]*Hominid Paleobiology Doctoral Program, Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, Washington, DC*
[3]*Department of Experimental Psychology, University of São Paulo, São Paulo, Brazil*
[4]*Department of Psychology, University of Georgia, Athens, GA*
[5]*Institute of Cognitive Sciences and Technologies, National Research Council, Rome*
[6]*Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, Washington, DC*
[7]*North Eastern Ohio Universities Colleges of Medicine and Pharmacy, Rootstown, OH*

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ABSTRACT The genus *Cebus* is one of the best extant models for examining the role of fallback foods in primate evolution. *Cebus* includes the tufted capuchins, which exhibit skeletal features for the exploitation of hard and tough foods. Paradoxically, these seemingly "specialized" taxa belong to the most ubiquitous group of closely related primates in South America, thriving in a range of different habitats. This appears to be a consequence of their ability to exploit obdurate fallback foods. Here we compare the toughness of foods exploited by two tufted capuchin species at two ecologically distinct sites; *C. apella* in a tropical rainforest, and *C. libidinosus* in a cerrado forest. We include dietary data for one untufted species (*C. olivaceus*) to assess the degree of difference between the tufted species. These data, along with information on skeletal morphology, are used to address whether or not a fallback foraging species exhibits a given suite of morphological and behavioral attributes, regardless of habitat. Both tufted species ingest and masticate a number of exceedingly tough plant tissues that appear to be used as fallback resources, however, *C. libidinosus* has the toughest diet both in terms of median and maximal values. Morphologically, *C. libidinosus* is intermediate in absolute symphyseal and mandibular measurements, and in measures of postcranial robusticity, but exhibits a higher intermembral index than *C. apella*. We propose that this incongruence between dietary toughness and skeletal morphology is the consequence of *C. libidinosus*' use of tools while on the ground for the exploitation of fallback foods. Am J Phys Anthropol 140:687–699, 2009. ©2009 Wiley-Liss, Inc.

WHY AND WHEN PRIMATES "FALLBACK"

Primates respond to seasonal variation in resource availability and abundance in a variety of ways including increasing travel rates (Doran, 1997), increasing the intensity of core area use (van Roosmalen, 1980; Sigg and Stolba, 1981), increasing or decreasing foraging party size (Doran, 1997; Matsumoto-Oda et al., 1998; Watts, 1998; Dias and Strier, 2003), increasing diet breadth (Heiduck, 1997; Hill, 1997; Overdorff et al., 1997; Knott, 1998; White, 1998; Gursky, 2000; Martins and Setz, 2000; Poulsen et al., 2001; Curtis, 2004) and shifting to fallback foods (McFarland-Symington, 1988; Leighton, 1993 Doran, 1997; Tutin et al., 1997; Conklin-Brittain et al., 1998; Yamakoshi, 1998; Wallace, 2005; Worman and Chapman, 2005).

The role of fallback resources in primate ecology and evolution has recently become a topic of particular interest to biological anthropologists (Lambert et al., 2004; Wright, 2004, 2005a; Scott et al., 2005; Lambert, 2007; Marshall and Wrangham, 2007). In earlier anthropological and primatological literature the concept of critical function (i.e., morphological features used during periods of resource scarcity) touched upon the role of fallback foods in primate evolution (Kinzey, 1978; Leighton and Leighton, 1983; Rosenberger, 1992; Constantino and Wright, 2009). The concept of fallback resource use has been linked directly to questions of community diversity,

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*Correspondence to: Barth W. Wright, Kansas City University of Medicine and Biosciences, 1750 Independence Ave, Kansas City, MO 64106-1453. E-mail: bwright@kcumb.edu

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food mechanics, morphological and behavioral specialization and, ultimately, selection pressures and evolutionary change (Constantino and Wright, 2009). Such inquiry has generated questions about the ability of primates to survive periods of resource scarcity, and about behavioral and morphological adaptations that may be critical for survival.

DEFINING FALLBACK FOODS

At the most general level, fallback foods may be defined as resources that are used when preferred foods are in low supply or are unavailable (Marshall and Wrangham, 2007; Constantino and Wright, 2009). Although the term "fallback foods" and the notion of "falling back" have a range of ecological and evolutionary implications (Constantino and Wright, 2009) we are operationalizing the term fallback foods in this study using the definitions proposed by Marshall and Wrangham (2007). Marshall and Wrangham (2007) distinguish between two subsets of fallback foods: "staple" and "filler." Staple fallback foods are defined as resources that are annually available, used throughout the year in small quantities, and may make up 100% of the diet during particular seasons. Filler fallback foods may be seasonally or annually available; are used only at particular times of the year and never comprise the majority of the diet. It is also of particular relevance to this study that resources that are termed fallback foods are often physically-challenging-to-exploit (Kinzey, 1974; Lambert et al., 2004; Wright, 2005a).

CEBUS AND FALLING BACK

Adaptations among capuchins species have been identified as critical functions for the use of particular resources that are in certain instances mechanically challenging to ingest (Kinzey, 1974). In fact, the capuchin foraging strategy can be broadly described as "destructive," due to its emphasis on easily digested food parts that are embedded in mechanically challenging tissues (e.g. palm fruits, colonizing insects, legume pods). The genus *Cebus* includes two morphotypes: the tufted capuchins, which exhibit relatively large teeth with the thickest dental enamel among primates (Kay, 1981; Wright, 2005a), as well as robust skeletal elements and musculature (Ford and Hobbs, 1996; Wright, 2007), and the untufted capuchins, which have relatively smaller teeth, slightly thinner enamel, and a less robust musculoskeletal system.

Various studies have detailed the differences between tufted and untufted capuchin species in gnathic morphology and have used their morphological findings to propose ingestive behavior. Bouvier (1986a) found greater mandibular corporal width and mandibular symphyseal robusticity in the tufted *C. apella* than in the untufted *C. albifrons* and *C. capucinus*. The relatively shallow mandibular corpus of *C. apella* along with intermediately tall incisors lead Bouvier to argue for an increase in mastication as opposed to incisor biting in *C. apella*. Greater corporal and symphyseal cross-sectional size and significantly thicker cortical bone on the lateral surface of the corpus and throughout the symphysis were also found to distinguish the tufted *C. apella* from the untufted *C. capucinus* (Daegling, 1992). These gnathic adaptations in *C. apella* were argued to better resist parasagittal bending, vertical bending at the symphysis, wishboning, and lateral torsion as demonstrated by Hylander (1985, 1988) and Hylander and Johnson (1994). Daegling (1992) argued that the morphological adaptations of *C. apella* may have evolved to resist high stresses during anterior dental use or during powerful/frequent mastication. Comparing the cranial morphology of *C. apella* and *C. albifrons*, Cole (1992, p 274) found that "The corporal shapes of the *C. apella* samples suggest greater resistance to both parasagittal bending and twisting (as predicted previously)." Cole in reference to Hylander (1988) argued that twisting causes the greatest stress regimes in the mandibular corpus, particularly when the primate in question exhibits wide zygomatics, as does *C. apella* (Masterson, 1996), and when the premolars are frequently used.

In a comparison of eight Neotropical primate species, Anapol and Lee (1994) found that *C. apella* exhibited the largest canine areas and the greatest postcanine occlusal areas (Anapol and Lee, 1994). Leverage for both the untufted *C. olivaceus'* and tufted *C. apella*'s masseter muscles were intermediate among all eight primate species, but their temporalis leverage was the highest. The mandibles of the capuchins had symphyseal depths and widths that were second only to those of *Chiropotes satanas*, and they had the greatest mandibular breadth, with intermediately wide mandibular corpora. Condylar heights of the capuchins were comparable to those of all other species, except the greatly exaggerated form characteristic of the mandibles of *Alouatta seniculus* (Anapol and Lee, 1994). The morphology exhibited by the capuchins was related to their relatively frugivorous diet that included relatively hard fruits.

Wright (2005a, p 476) noted that the findings of these previous studies "could be used in a variety of combinations to argue for dependence on the postcanine teeth (e.g., large postcanine occlusal area and wide mandibles) or on the incisors and canines (e.g., robust canines, wide incisors, and temporalis advantage)." Wright (2005a) found that the tufted *C. apella* had greater jaw adductor leverage and canine and incisor cross sectional areas than the sympatric untufted *C. olivaceus* and thicker molar enamel than the untufted *C. olivaceus*, *C. albifrons*, and *C. capucinus*. When coupled with data on ingested and masticated food tissues from the wild, Wright (2005a) argued that the craniodental complex of *C. apella* has various biological roles permitting the processing of soft foods as well as reliance on the anterior teeth for breaching mechanically demanding foods and occasional cheek tooth biting of exceedingly tough foods. Wright's (2005a) findings reveal that the biological role of the gnathic features of any primate can only be identified when coupled with ecological data from the field. Without such data a seeming paradox, comparable to that proposed by Liem (1980) for African cichlid fishes, may be the interpretive result, i.e. the anatomical features of the tufted capuchins may be seen as niche narrowing specializations for the exploitation of hard and tough foods, yet the tufted capuchins belong to the most ubiquitous group of closely-related primates in South America, successfully inhabiting a wide range of different environments.

Beyond the differences in gnathic morphology that have been identified in tufted and untufted capuchins, previous work has also shown that tufted and untufted capuchins differ in postcranial morphology. As is the case with their crania, tufted capuchins exhibit robust postcranial elements compared to their gracile untufted congeners (Jungers and Fleagle, 1980; Ford and Hobbs, 1996; Llorens et al., 2001; Wright, 2005b, 2007). In addition, tufted capuchins have a slightly shorter torso than untufted capuchins (Hershkovitz, 1949), smaller joint surfaces, and relatively shorter distal limb elements (Ford and Hobbs, 1996; Wright, 2005b, 2007). The postcranial morphologies in tufted capuchins have been largely attributed to their slower, more deliberate mode of arboreal quadrupedalism (Fleagle and Mittermeier, 1981; Wright, 2005b, 2007), however some of these differences, such as variation in relative limb segment lengths, may well be attributable to foraging behavior. In a comparative study linking differences in postcranial morphology to differences in patterns of locomotor behavior in the tufted *C. apella* and the untufted *C. olivaceus*, Wright (2007) found comparable frequencies of climbing behavior between these two species and yet relatively short hind limbs and short tibiae in *C. apella*. Relatively short hind limbs and tibiae have been argued to facilitate climbing (Cartmill, 1985; Jungers, 1977). Wright (2005b, 2007) suggested that this incongruity between behavior and morphology was best explained by the frequent use of postures and movements associated with specific foraging behaviors, particularly the breaching of hard and tough food items (i.e., nut-cracking). Manual hard fruit cracking has been well-documented in wild tufted capuchins (Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Fragaszy et al., 2004a) and having relatively short limbs, overall, in addition to relatively shorter hind limbs, may provide a mechanical advantage particularly when using rocks to crack palm fruits on the ground (Liu et al., 2009).

The possibility of identifying a disassociation between seemingly specialized morphology and niche breadth in capuchins is reminiscent of the same disassociation identified by Liem (1980) in cichlid fish communities (Robinson and Wilson, 1998). In modeling these fish communities, Robinson and Wilson (1998) demonstrated that the ability to forage optimally on a particular subset of foods unique to each forager did not limit each species dietary breadth, but rather broadened the resources available to them. Ultimately, these authors suggested that their model may be relevant only to aquatic environments and they questioned the possibility of a broader application of their model to terrestrial communities. However, there is evidence to suggest that their model may provide an explanation for how tufted capuchins are able to exist over such a large geographic area, succeed within diverse primate communities, and successfully exploit a broad range of habitats. Wright (2004, 2005a) found that the average toughness of foods ingested by six primate species, *Pithecia pithecia*, *Chiropotes satanas*, *Ateles paniscus*, *Alouatta seniculus*, *Cebus olivaceus*, and *Cebus apella*, did not significantly differ. However, *C. apella* ingested and masticated a few foods with extreme toughness values and with maxima of greater than 10,000 J m^{-2}. The maximum toughness value for *C. apella* was roughly 10 times the average value for all six study species (including *C. apella*). Wright (2004, 2005a) argued that, as with the cichlids, the masticatory adaptations of *C. apella* actually broadened, rather than restricted, their dietary niche. Likewise, interpretations of the biological role of the postcrania in tufted capuchins suggest that their relatively shorter hind limbs and robust limb elements assist in the successful procurement of foods in a broad variety of variably seasonal environments (Wright 2005b, 2007), revealing another suite of niche-broadening characters.

The present study represents initial analyses within the context of a larger research program that seeks to obtain seasonal data on feeding frequencies, food mechanics, food size, and ingestive behavior among tufted capuchins in various habitats that differ in terms of their resource base, geography (e.g. altitude), and seasonality. Our goal is to use these data, along with information on skeletal morphology, to test whether this supposedly quintessential fallback foraging taxon exhibits a given suite of morphological and behavioral attributes regardless of habitat. We also ultimately seek to assess whether individuals that can more readily exploit fallback foods gain a fitness advantage. It is of note that other primate taxa such as *Gorilla gorilla gorilla* (Yamagiwa, 2009) *Cercocebus* spp. and *Lophocebus* spp. (Fleagle and McGraw, 1999; Lambert et al., 2004), *Papio* spp. and *Mandrillus* spp. (Altmann, 1998; Fleagle and McGraw, 1999) and *Rhinopithecus* spp. (Covert et al., 2008; Le et al., 2006; Grueter et al., 2009) to name a few, appear to be species that could provide compelling comparative data to relate to those collected here on *Cebus*.

In this study we measure the dietary toughness of two tufted capuchin species that inhabit an evergreen tropical rainforest (*C. apella*, east bank of the Essequibo River adjacent to Turtle Mountain, Iwokrama Reserve, Guyana) and a cerrado-caatinga dry ecotone forest (*C. libidinosus*, Boa Vista, Piauí, Brazil). We evaluate the relative difference in dietary toughness between the two tufted species by comparing both to the dietary toughness of an untufted capuchin species, *C. olivaceus*, from the west bank of the Essequibo River at the site of Turtle Mountain, in the Iwokrama Reserve, Guyana. Although we can not yet assess the exact frequency with which the tufted capuchins exploit mechanically demanding fallback resources at each site, at Turtle Mountain, the tufted capuchins appear to exhibit a staple fallback strategy that focuses on woody legume pods and colonizing insects in woody substrates, with little evidence of fallback palm fruit use. At Boa Vista the tufted capuchins also appear to exhibit a staple fallback strategy focusing on palm fruits. It is of particular note that the kernels of the hardest palms exploited at Boa Vista are accessed by inducing initial cracks with rock hammers and wooden or rock anvils in a terrestrial setting (Fragaszy et al., 2004a; Visalberghi et al., 2005, 2007; Madden et al., 2007; Ottoni and Izar, 2008).

PREDICTIONS

Given Wright's (2004) findings we predict 1) that the average dietary toughness will be comparable for each species, and 2) the tufted species will include a limited number of exceedingly tough plant tissues in their diets. As a consequence of predictions 1 and 2, the distributions for the toughness of processed tissues will exhibit a positive skew (i.e., long right-hand tails) for the tufted species due to the inclusion of tough fallback foods, but the distributions for all three species will have comparable central tendencies (i.e., median values). Given *C. libidinosus*' well documented palm fruit foraging behavior, which includes the use of stones and anvils for crushing, we further predict, 3) that this tufted species will process the toughest food items and as a consequence will have the most robust jaws and postcranial skeletons. The use of stone tools by *C. libidinosus* is also predicted 4) to be associated with relatively long forelimbs for increased velocity when bringing rock hammers toward the palm fruit to be cracked, and shorter hind limbs for enhanced biomechanical advantage when lifting heavy rock hammers.

MATERIALS AND METHODS

Study sites

As previously noted, two sites that differed markedly in rainfall, forest physiognomy, and phenology were chosen for this study to determine the degree to which fallback strategies vary among tufted capuchins when in distinct habitats. The east bank of the Essequibo River, across this major waterway from the site of Turtle Mountain, Iwokrama Reserve, Guyana (5°01N, 55° 34′W) is inhabited by the tufted *C. apella*. *Cebus olivaceus* was observed on the west bank of this major waterway, at the site of Turtle Mountain, within the reserve. Each research area consisted of ~100 km of trails along a 12,200 ha park including a 530 m (asl) mountain, and exhibits evergreen tropical montane and lowland forest (Wright, 2004, 2005b, 2007). The forests on either side of the river were comparable in terms of tree species availability, abundance, and forest structure (Wright, 2004, 2005b, 2007). The site of Fazenda Boa Vista, Piauí, Brazil (9° S, 45°W, about 450 m asl), is dominated by dry caatinga-cerrado forest and woodland and is home to the tufted species, *C. libidinosus*. This site is covered by ~100+ km of meandering trails. The low canopy and more open nature of the vegetation at Boa Vista make *C. libidinosus* easier to observe in close proximity, as opposed to the difficulties of observing *C. apella* in the rainforest environment, particularly during the dry season.

Foods and food processing behavior

Uningested parts of foods processed by adult individuals were collected for mechanical analysis and their tissues were classified according to the manner in which they were handled. Given the dense canopy and typically greater than 10 m viewing distance in Guyana, food tissues were placed into only two primary categories: mastication and ingestion. The former referred to tissues being chewed in the oral cavity with the cheek teeth. The latter was divided into three subcategories at Boa Vista, where the viewing distance is often less than 5 m and in more open terrain. These categories included use of the incisors and/or canines without the hands; use of the incisors and/or canines with the hands; use of the hands alone. Use of the hands alone typically involved using the entire forelimb, and in the case of nut cracking with hammers at Boa Vista, ingestive behavior involved the entire body. Given the limited number of food tissue processing categories for the data from Guyana we pooled the ingest categories from Boa Vista for analysis.

The physical properties of food tissues do not survive long-term storage and must be estimated while in the field. The best way to preserve most foods in the field is to place them in plastic bags with damp paper towels to preserve moisture content. Foods were tested within 12 h of collection. A comparison in Vietnam of the material properties of leaves bagged for 12 h, left open to the air for 12 h, and immediately tested revealed no significant difference between the toughness of bagged and immediately tested leaves (Wright, unpublished data).

Food mechanics

During mastication, fragmentation of food between the teeth is largely dependent on either the food's toughness or a combination of its toughness and stiffness, expressed as fragmentation indices (Agrawal et al., 1997; Lucas et al., 2002). Given the need to process samples quickly in Guyana, and limited time at Boa Vista, we focused on the acquisition of toughness data using scissor cutting, the samples for which are quickly made and the tests are quickly conducted (Wright, 2005a). Toughness is defined as 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; Vincent, 1992; Lucas, 2004). Food tissues that can withstand high strains before crack propagation are termed displacement limited (Lucas et al., 2000). Leaves are the quintessential displacement limited foods in the diets of primates, yet they are also thin and demand relatively little force to tear with the hands, however, they demand repetitive slicing with the molars to produce enough small pieces for adequate breakdown by gut fauna. Tissues that are typically breached to access less mechanically demanding digestible components are often highly stress limited (i.e. they can withstand relatively high forces with little strain, yet often catastrophically fail at a given threshold). It has also been shown that the degree to which a food or food tissue falls in the displacement or stress limited category may be expressed as a ratio between the toughness of the given tissue and its stiffness or Young's modulus (Lucas et al., 2000; Williams et al., 2005). In this study we focus on only one of these two variables (i.e. toughness) and future analyses will include data on the stiffness of tissues ingested by these species as well as their respective ratios. Tufted capuchins have been noted to crack hard and seemingly stiff palm fruits with their teeth (Terborgh, 1983). This requisite morphology, and thus the ability to orally process stiff fallback foods, may be the primary characteristic differentiating tufted from untufted capuchins, and differentiating species of tufted capuchin, however, it is of note that structurally complex foods, such as palm fruits often have accessory struts that arrest cracks or have multiple tough layers. Thus we feel that toughness alone is an apt measurement for comparing the mechanical demands that a food poses for a feeding primate.

All toughness tests were conducted using a portable universal tester, described originally by Darvell et al. (1996). The tester is fitted with 10 N and 100 N load cells and furnished with attachments described by Lucas et al. (2001). This machine resembles a portable "Instron-type" universal testing machine found in engineering, materials science, and food science laboratories, and has been used in ecological studies for over 10 years, being successfully used by various researchers in the field (See www.gwu.edu/~hebdp/fieldtech for description of the machine, its applications, and additional references. Also see Lucas et al., 2001; Lucas, 2004).

Cranial and postcranial morphology

We conducted preliminary comparisons of mandibular and limb robusticity as well as limb intermembral indices among the three capuchin species to test hypotheses linking cranial and postcranial morphological variation with observed variation in ingestive and processing behavior. Data were collected on specimens housed at the Field Museum of Natural History, the American Museum of Natural History, and at the National Museum of Natural History, USA. Two wild-caught specimens of *C. olivaceus* were obtained from the Georgetown Zoo, Georgetown, Guyana. Although the provenance of the museum specimens did not permit us to measure individuals from the exact field study sites, specimens for this study were chosen based on several criteria. Specimens of *C. apella, C. libidinosus,* or *C. olivaceus* were chosen based on the habitat type that the specimen was collected from (wet tropical rainforest for *C. apella* and *C. olivaceus* or cerrado-caatinga forest for *C. libidinosus*), and, when possible, collected from Guyana (*C. apella* and *C. olivaceus*) or areas nearest to the state of Piaui, Brazil (*C. libidinosus*). All cranial specimens were collected in Guyana (*C. apella* $n = 14$ and *C. olivaceus* $n = 17$), or the cerrado-caatinga region of Brazil (*C. libidinosus* $n = 17$). Several postcranial specimens for *C. apella* ($N = 7$) were collected in Guyana or western Suriname, from highly comparable, if not identical, habitats (Mittermeier and van Roosemalen, 1981; Wright, 2005b). Because of a relative lack of available postcranial specimens, and in order to generate a reasonable sample size, we also included postcranial specimens of *C. apella* from other wet tropical rainforest habitats in Colombia ($N = 7$) and Peru ($N = 11$). All specimens of *C. olivaceus* were collected in Guyana ($N = 9$) and eastern Suriname ($N = 1$). To address the issue of body size, we turned to published body weights for the three species, which indicate that they are comparable (Ford and Davis, 1992; Smith and Jungers, 1997). In addition, we compared log transformed geometric means between groups (i.e., *C. apella—C. libidinosus, C. apella—C. olivaceus,* and *C. libidinosus—C. olivaceus*) to test for differences in body size within our sample. In this case, comparisons of relative limb proportions and the use of limb bone length to standardize bone breadth dimensions requires comparable body size among the three study species (Schultz, 1953; Ruff, 1987). The literature suggests that the three species are similar in body size, however, to confirm this for our sample, we constructed a geometric mean (Sokal and Rohlf, 1995) from a series of 22 measurements of postcranial elements (humerus, ulna, femur, and tibia) for each individual. The geometric mean is a measure of total size that is commonly used in morphometric studies as a substitute for, or in addition to, body mass or other single variable proxies of body size (Jolicoeur, 1963; Bonner, 1965; Mosimann, 1970; Mosimann and James, 1979). The choice of variables to include in the construction of a morphometric geometric mean is dependent on both the question at hand and the taxa of study (Mosimann and James, 1979; Reist, 1984; Jungers et al., 1995), and it is generally held that a large number of measurements appropriate to the anatomical complex in question will produce a reliable estimate of body size (e.g. a morphometric geometric mean constructed of cranial measurements might be an inappropriate estimate of size for a study concerned with postcranial variation, as size-related changes in postcranial shape are most likely best related to changes in postcranial size, as opposed to changes in skull size). No significant differences in body size were identified for any of the three comparisons (Student's t, $P > 0.05$).

We compared log transformed mandibular symphyseal height and width and mandibular depth and width (at M_2) (Bouvier, 1986a,b) with the Student's t statistic. We compared these measures set relative to mandibular length to assess shape differences and we compared absolute measures of these features. The linear external measurements used in this study do not necessarily fully capture the internal geometry of the jaw (Daegling, 1989, 2002; Vinyard and Ryan, 2006). Since these are maximum rather than minimum linear measures they also prohibit direct inference of maximum stress at the corpus or symphysis. However, Daegling, 1992 demonstrated that the tufted *C. apella*, shown previously by Bouvier (1986a) to have relatively externally robust corpora and symphyses, also exhibited more robust cross sections in these regions that differ from the untufted *C. capucinus* primarily in size as opposed to shape. While it has been shown that load resisting ability is more accurately captured through measuring cross-sectional morphology, we suggest that these linear measures represent a strong first approximation in comparing the load resisting abilities of the three capuchin species (see also Hylander, 1979, 1988; Smith et al., 1983; Bouvier, 1986a,b; Ravosa, 1991, 1996; Cole, 1992; Anapol and Lee, 1994; Taylor, 2002; Vinyard et al., 2003; Plavcan and Daegling, 2006).

We compared maximum forelimb and hind limb lengths and intermembral indices for these species, as well as two ratios of humeral and femoral robusticity (AP width at midshaft divided by maximum length and ML width at midshaft divided by maximum length). Measurements of long bone robusticity using external shaft diameters or cross-sectional geometry provide a means for assessing the relative strength of a bone and its resistance to bending and compressive forces, with variation in robusticity reflecting differences in mechanical loading regimes and functional adaptations (Ruff et al., 2006; Stock and Shaw, 2007). In this study, we used both AP and ML diaphyseal thickness standardized to bone length as an indicator of skeletal robusticity and as a preliminary measure of humeral and femoral bone strength in the three capuchin species. Given that the three species are comparable in both body size and body mass, and the sample specimens are comparable in size, this method provides a means by which to make preliminary comparisons of bone robusticity and strength among the three species (Schultz, 1953; Ruff, 1987, 2000; Polk et al., 2000; Stock and Shaw, 2007). We do however recognize that diaphyseal circumference is preferred over diaphyseal breadths for inferring bone strength when cross sectional dimensions are not available (Stock and Shaw, 2007), and therefore interpret these initial findings with caution. The parametric Student's t test was used for comparison of natural log transformed limb lengths while the nonparametric Mann Whitney U test statistic was used for comparison of indices and ratios.

Data analysis: Dietary toughness

The predictions presented above are based on empirically-observed distributions of toughness values for six species of Neotropical primates in Guyana (Wright, 2004). These distributions show comparable central tendencies (i.e. the average and median toughness values are broadly similar). They differ, however, in that certain species, such as those exhibiting masticatory specializations for consuming foods with challenging mechanical properties (e.g., *C. apella* and *A. seniculus*) exhibit right skews for their toughness distributions. The long right-hand tails indicate the exploitation of a few exceedingly

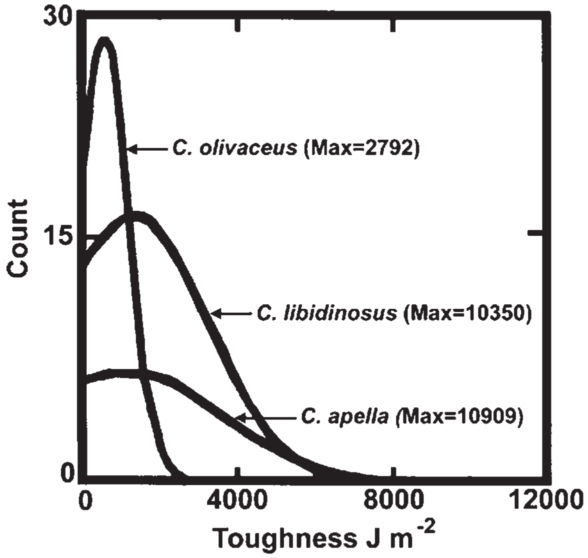

Fig. 1. Distributions of toughness values for tissues masticated by all three capuchin species. The distributions are labeled with species names and arrows. Maximum toughness values are in parentheses. Note the comparable means, but the wider distributions with longer right hand tails for the tufted *C. apella* and *C. libidinosus*. This is indicative of their mastication of a few extremely tough tissues.

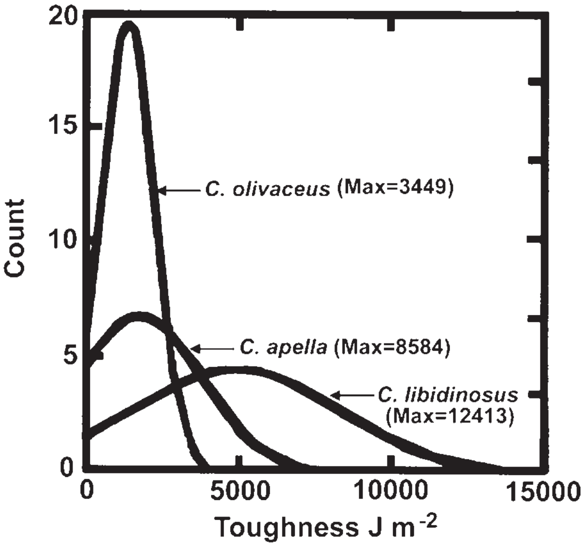

Fig. 2. Distributions of toughness values for foods processed manually and/or with the anterior dentition by all three capuchin species. The distributions are labeled with species names and arrows. Maximum toughness values are in parentheses. Note the comparable means, but the wider distributions with longer right hand tails for *C. apella* and *C. libidinosus*. This is indicative of their ingestion of a few extremely tough tissues, particularly in the case of *C. libidinosus*. Note the markedly higher ingested tissue maxima for *C. libidinosus* ($P < 0.05$ compared to both species using bootstrap methods).

tough items. These food items have been argued (Wright, 2005a) to represent fallback items that, although exploited infrequently, have placed important selective pressure on their feeding apparatuses. Thus, we performed statistical tests that compared both the central tendency of toughness values and maximal values among species. We opted for a nonparametric two-sample test (Mann-Whitney U) to compare the central tendency of these distributions among species. We chose this statistic rather than the parametric Student's *t* statistic due to the heteroscedastic nature of the distributions.

To compare maximal toughness values between two species, we developed a randomization approach because the distribution of maximum toughness values are not well characterized. Initially, toughness values from the two species being compared are combined. Two distributions (equal in size to the samples of toughness values for the two species being compared) are drawn at random with replacement from this pooled sample. The difference in maximum values between these two distributions is quantified. This sampling procedure was repeated 1,000 times to generate a distribution of randomly generated differences in maximum toughness values. If the observed difference in maximum toughness values between the two species exceeded the 95th percentile from this bootstrapped distribution, we rejected the null hypothesis of no difference in maximum toughness values between species. All test statistics were run in Systat 11.0.

RESULTS

Masticated tissues

We divided processed tissues into "masticated" (those that were chewed and ultimately swallowed) and "ingested" (those that typically encase the masticated tissues and are opened with the hands alone, the anterior dentition alone, or the hands and anterior dentition). Ingested tissues significantly exceeded masticated tissues in toughness (Mann-Whitney U, $P < 0.01$) when pooled for all species and when ingested and masticated tissues were compared for each capuchin species (Mann-Whitney U, $P < 0.01$ for each comparison). In order from the highest mean (and median) masticated toughness to the lowest mean (and median) masticated toughness, *C. libidinosus* ($N = 15$) exceeded *C. apella* ($N = 14$), which exceeded *C. olivaceus* ($N = 17$). However, *C. libidinosus* only significantly exceeded *C. olivaceus* ($P < 0.05$). *C. apella* was found to masticate the toughest single food tissue (see Fig. 1). However, the randomization test comparing differences in maximum values did not identify a significant difference between any of the species pairs. It is worth noting that despite the lack of significant difference the distributions of toughness data for the two tufted species are much broader with longer right-hand tails than that of *C. olivaceus* (see Fig. 1). This is a consequence of the tufted species mastication of a few exceedingly tough tissues.

Ingested tissues

C. libidinosus ($N = 15$) ingested significantly tougher tissues than both *C. apella* ($N = 14$) and *C. olivaceus* ($N = 17$) on average ($P < 0.01$). *C. libidinosus* also ingested the maximally toughest tissue, followed by *C. apella* and *C. olivaceus* (see Fig. 2). The difference between the maximum values for *C. libidinosus* relative to *C. olivaceus* was significant ($P < 0.05$). The distributions for all three species appear similar to those for masticated tissues, however that for *C. libidinosus* is markedly broader than that for *C. apella* and the central tendency is also significantly higher.

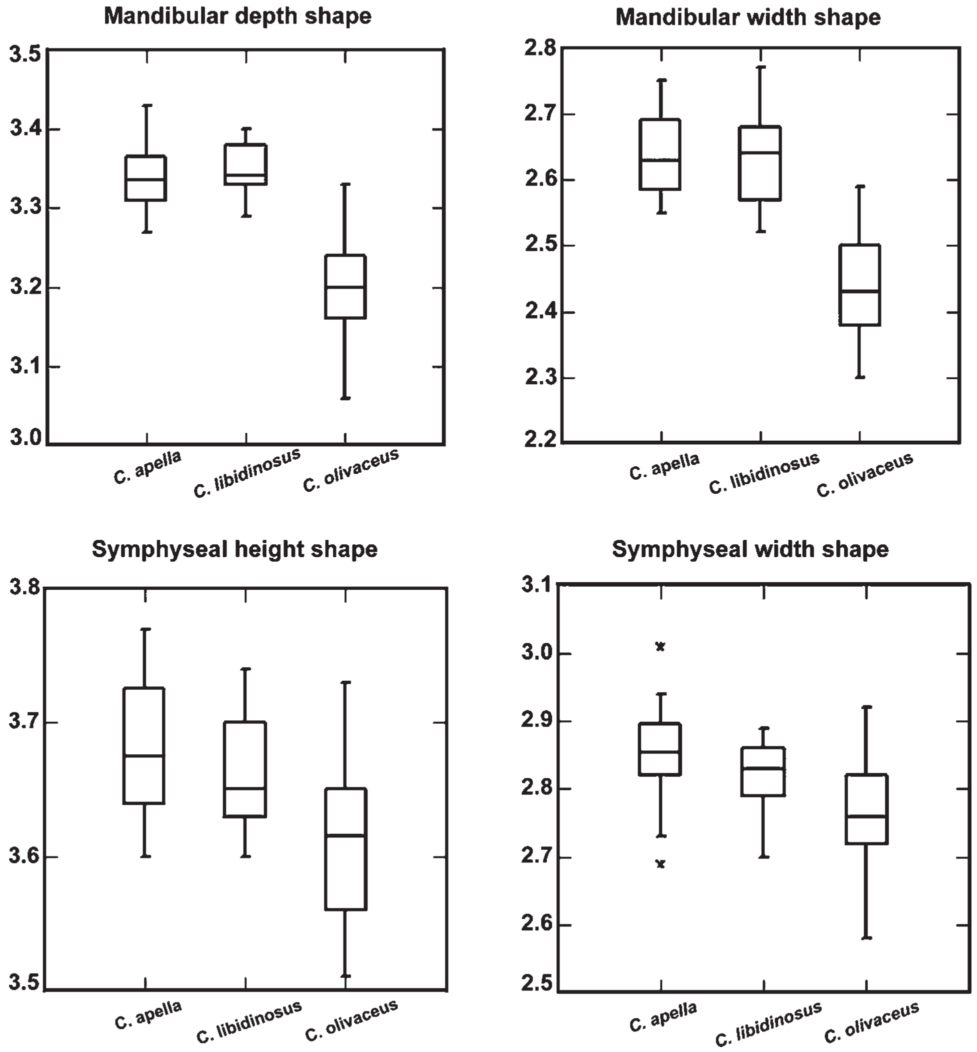

Fig. 3. Box and whisker plot comparing log normal values for four mandibular measurments relative to mandibular length. Horizontal center line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles.

Jaw morphology

When mandibular corpus and mandibular symphysis measures are set relative to mandibular length we find that the tufted species (*C. apella* $N = 25$ [12 female, 13 male], *C. libidinosus* $N = 35$ [17 female, 18 male] do not differ significantly, and both tufted species significantly exceed ($P < 0.05$) the untufted *C. olivaceus* ($N = 30$ [14 female, 16 male]) (see Fig. 3). Wright (2005a) pooled tufted species in a comparison of load (jaw length) and lever (temporalis and masseter) lengths between tufted capuchins and *C. olivaceus* and found the tufted species to have significantly greater leverage for the temporalis and masseter muscles. Further comparisons of relatively small samples between each pair of the three species in this study (*C. olivaceus*, $N = 42$; *C. apella*, $N = 9$; *C. libidinosus*, $N = 13$) revealed only one significant difference, with *C. apella* exceeding *C. olivaceus* in masseter muscle leverage (Mann-Whitney U, $P < 0.01$). These findings are in line with those for mandibular robusticity. However, when absolute measures are compared among these three comparably-sized primates (Smith and Jungers, 1997; Fragaszy et al., 2004b), *C. apella* exceeds both *C. libidinosus* and *C. olivaceus* with high significance ($P < 0.01$) in every case (Fig. 4). In addition, *C. olivaceus* and *C. libidinosus* have comparable symphyseal measures.

Postcranial morphology

Our preliminary analysis of relative limb robusticity reveals comparable levels of robusticity for both the fore- and hind limb among all three species. Both tufted species are slightly more robust than their gracile congener, but they do not differ significantly from one another, nor do they differ significantly from the untufted *C. olivaceus* ($N = 10$ [5 female, 5 male]) (see Fig. 5). The similarity in robusticity between the tufted capuchins and the untufted *C. olivaceus* corroborates the findings of Ford and Hobbs (1996) which highlight the apparent intermediacy of *C. olivaceus* within the spectrum of gracile and tufted capuchin postcranial robusticity. The pattern for absolute limb lengths is similar to that for absolute mandibular measures. *C. libidinosus* ($N = 8$ [2 female, 6 male]) is intermediate in total humeral and total femoral lengths (see Fig. 6). *C. olivaceus* has the longest limbs, while

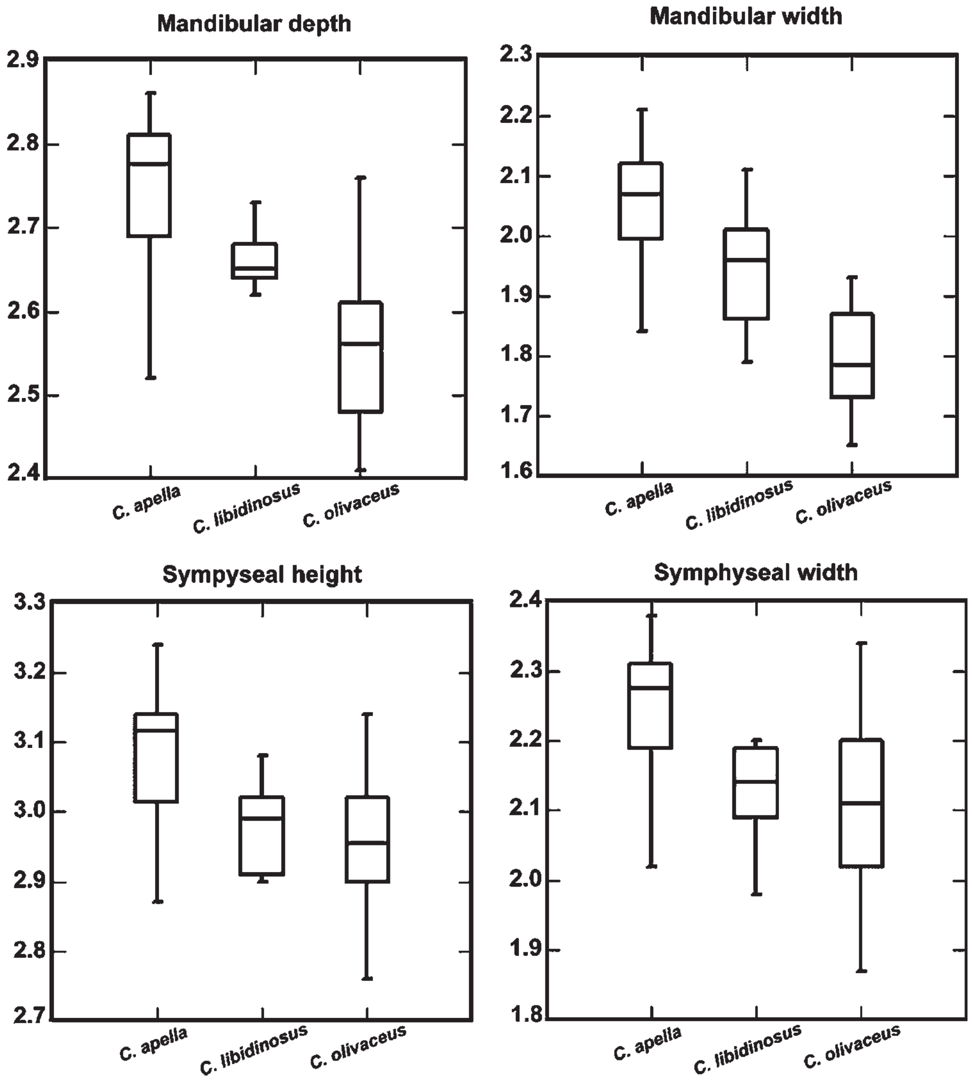

Fig. 4. Box and whisker plot comparing log normal values for four absolute mandibular measurments. Horizontal center line = median, length of box = range within which the central 50% of the values fall, hinges = first and third quartiles.

C. apella has the shortest limbs. *C. apella* (N = 25 [8 female, 17 male]) also has relatively short hind limbs when compared to the untufted *C. olivaceus* and to *C. libidinosus*. *C. libidinosus* is, in turn, intermediate between *C. apella* and *C. olivaceus* in relative hind limb length (see Fig. 6)

DISCUSSION

We found that the central tendency for the toughness of masticated items was comparable for all three species, however the inclusion of very tough ingested tissues by *C. libidinosus'* lead to a significantly greater overall toughness and maximal toughness for this species. As predicted, *C. libidinosus* includes some food items in its diet that are potentially more difficult to breach than those eaten by *C. apella*. In turn, the two tufted species included a few exceedingly tough masticated and ingested tissues in their diet, indicative of a dietary strategy that is marked by the inclusion of mechanically demanding fallback foods. Given these patterns for food toughness, we expected that *C. libidinosus* would exhibit the most robust jaws for the dissipation of high masticatory loads, particularly when using the front of the mouth, and we expected a more robust postcranial skeleton with rugose muscle marking for the vigorous and powerful manipulation of fallback items. Our preliminary data on jaw shape and size, postcranial robusticity and relative limb segment lengths reveals that this is not the case, and suggests that *C. libidinosus*, lacking the requisite jaw morphology, must rely on behaviors that include manual processing of food items that includes the use of tools.

How is it that the capuchin species with the toughest diet, in terms of central tendency and maximum values, has a cranial and postcranial skeleton that is intermediate in traits indicative of the ability to produce high muscular forces and dissipate high reaction forces? We presently hypothesize that this is a consequence of *C. libidinosus'* relatively high degree of terrestriality and their propensity to use tools when exploiting mechanically challenging fallback foods. A perfect example of this is *C. libidinosus'* exploitation of ubiquitous, but mechanically challenging palm fruits, which appear to

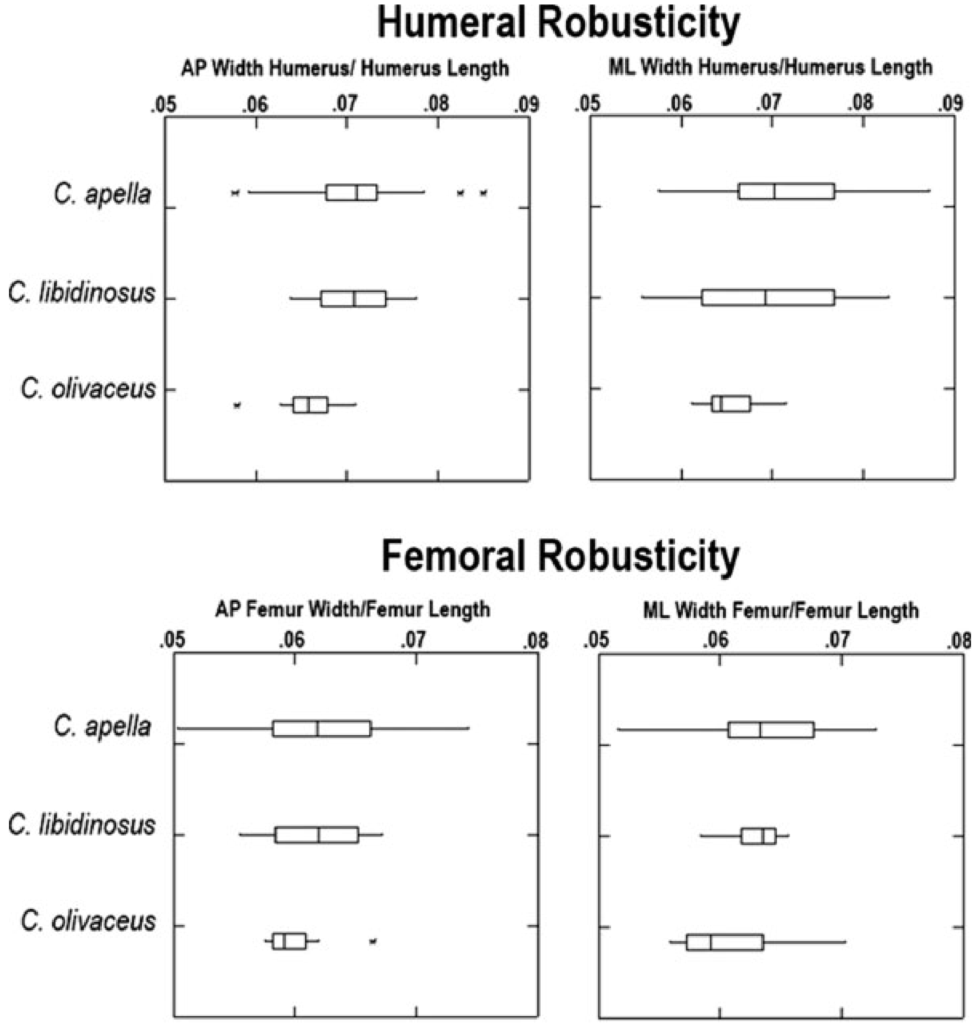

Fig. 5. Box and whisker plots comparing humeral and femoral robusticity in *C. apella* (n = 25), *C. libidinosus* (n = 8), and *C. olivaceus* (n = 10).

be the quintessential example of staple fallback resources for this capuchin species. These foods, the majority of which grow close to the ground, and which are exceedingly tough and hard, are initially cracked through the use of stone hammers and anvils at the site of Boa Vista (see Fig. 7). Cracked palm fruits are frequently further opened by using the anterior dentition and hands or the cheek teeth and hands. This use of tools appears to extend to foods that offer a mechanical challenge, but not a challenge that requires the use of tools for breaching. For example *Eschweilera* sp. pyxidia may be hit with stones at Boa Vista by *C. libidinosus* while they are opened with the anterior and/or cheek teeth and hand by *C. apella* in Guyana (Wright, personal observations). Thus, the relatively less robust mandibles seen in *C. libidinosus* may be due to relaxed selection accompanying the use of stone tools for the processing of mechanically challenging foods, or to increased selection for a more powerful masticatory system in the non-tool using *C. apella*.

From a physiological perspective, the finding that *C. libidinosus*, which from a relatively young age routinely lifts heavy stones as part of their foraging repertoire (Fragaszy et al., 2004a), do not have the most robust skeletal elements is somewhat counterintuitive. Previous work has shown that even moderate levels of routine exercise increases levels of circulating growth hormone (GH) in the bloodstream, leading to a global response in the skeletal system, thereby producing greater robusticity in the crania and postcrania. This finding has been used to argue that variation in robusticity levels among individuals may be caused by epigenetic factors (Leiberman, 1996). Given Leiberman's (1996) argument one would predict that *C. libidinosus* would have a more robust skeleton than *C. apella*, given routine lifting of heavy stones throughout much of its developmental period and through adulthood (Fragaszy et al., 2004a). However, there are data to suggest that all tufted capuchins have relatively robust skeletons both cranially (Cole, 1992) and postcranially (Jungers and Fleagle, 1980) from birth. Thus, variation in skeletal robusticity among tufted capuchins is likely due to selection on the postcranial skeleton brought about by variation in positional behavior (possibly foraging behavior) among sites, as opposed to variation in levels of activity over the lifespan of individuals.

While measures of postcranial robusticity do not support the prediction that differences in processing behaviors (oral versus manual) would be reflected in the postcranial skeleton, there appears to be some congruence

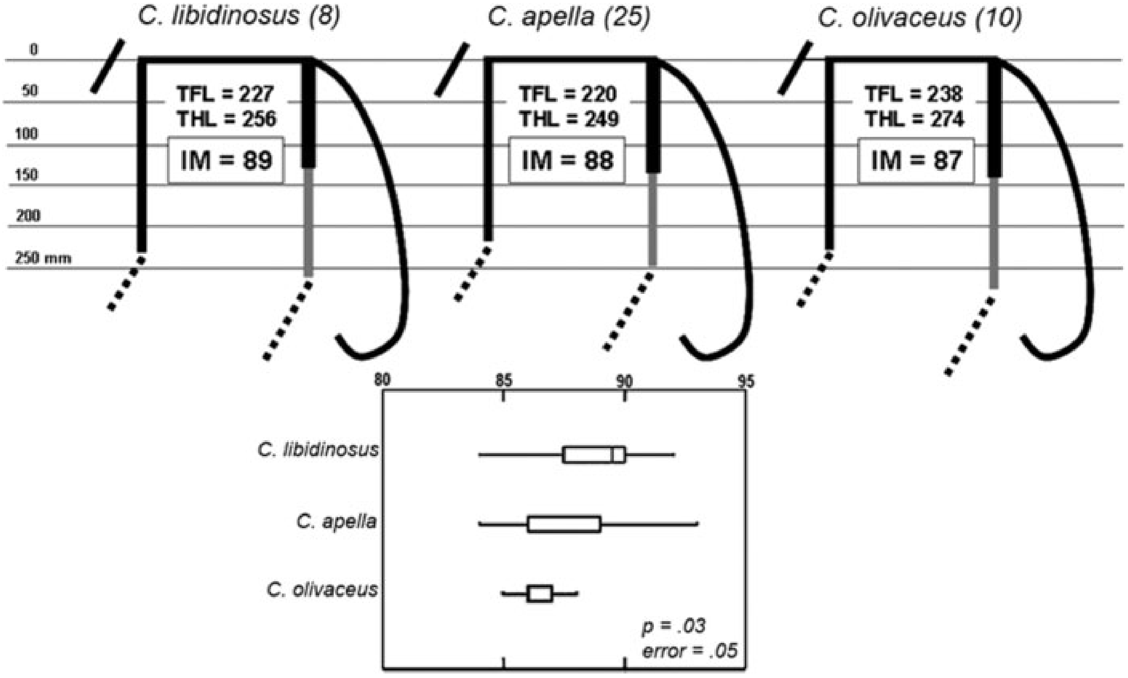

Fig. 6. Comparison of limb lengths and relative limb proportions in *C. libidinosus* (*n* = 8), *C. apella* (*n* = 25), and *C. olivaceus* (*n* = 10) using diagrammatic figures and a box and whisker plot. TFL = total forelimb length, THL = total hind limb length, and IM = intermembral index. Box and whisker plot compares IM index among the three species.

Fig. 7. Adult male *C. libidinosus* cracking half a palm fruit (*Attalea* sp.) at Fazenda Boa Vista. Photo by Barth W. Wright.

between absolute and relative limb lengths and foraging behavior among the study species. *C. libidinosus* at Boa Vista have been found to spend approximately one third of their time on the ground (Verderane, unpublished data) and, as previously noted, the palms that it exploits are found in bundles close to the ground, which demands more terrestrial foraging. *C. libidinosus* may have limbs that are intermediate in length between *C. olivaceus* and *C. apella* due to increased terrestriality. The untufted *C. olivaceus* appear to have the longest limbs to permit it to move greater distances in a day and more quickly in an arboreal environment (Wright, 2005b). *C. apella*'s relatively short limbs pull its center of gravity closer to the substrate when traveling and foraging in a slower more deliberate manner in an arboreal habitus (Wright, 2005b). It is also of note that *C. libidinosus* forages and travels in a deliberate manner, but much of its positional behavior occurs on the ground were there is less chance of falling.

Wright (2007) found that tufted capuchins have relatively short hind limbs when compared to the untufted *C. olivaceus*. Although Wright (2007) pooled tufted species for analysis, the preliminary results of the present study corroborate these findings, while providing additional information for the development of testable hypotheses. *C. apella* appears to have relatively shorter hind limbs than *C. libidinosus*. *C. libidinosus* is, in turn, intermediate between *C. apella* and *C. olivaceus* in relative hind limb length. We entertain three possible explanations for these differences. *C. apella* may be derived in terms of relative limb lengths, permitting manual processing of hard food items in an arboreal setting. On the other hand, *C. libidinosus*, with slightly longer forelimbs relative to hind limbs may exhibit a derived version of the tufted postcranial pattern allowing it to more efficiently use stones and anvils in a terrestrial as opposed to arboreal setting. Citing Wright's (2007) study, Liu et al. (2009), in an analysis of the kinematics of nut-cracking in *C. libidinosus* (also conducted at the site of Boa Vista, and using the same population of capuchins examined in this study), further suggest that the relative lengths of the fore- and hind limbs in *C. libidinosus* facilitates more efficient movement during stone hammer and anvil use when nut cracking. The question of whether the slightly longer limbs of *C. libidinosus* are an adaptation for semi-terrestriality that has been exapted for more efficient hammer and anvil nut cracking (or vice versa) is a question that we are currently investigating.

It is additionally possible, given that a relatively longer forelimb enhances climbing efficiency (Jungers, 1977; Cartmill, 1985), that *C. libidinosus* climbs more than other tufted species. It is of note that the terrestrial substrates used by *C. libidinosus* at Boa Vista include large outcroppings of rock and cliff faces that require frequent climbing when moving across sparsely forested parts of their habitat. A test of this final hypothesis, and exploration of the multiple selective factors that may interact in shaping the behavioral repertoire and postcranial form of *C. libidinosus* at Boa Vista, are currently underway. We additionally plan to offer both *C. apella* and *C. libidinosus* foods with comparable mechanical and physical properties, as well as tools for their exploitation, and see how they are processed.

CONCLUSIONS

1. Both tufted species incorporate mechanically challenging staple fallback tissues/foods in their diet.
2. The more craniofacially gracile of the two tufted species (*C. libidinosus*) has the tougher diet as measured by median and maximum values. This uncoupling of morphology and food mechanics is hypothesized to be a consequence of *C. libidinosus'* use of stone tools when processing mechanically challenging foods.
3. The long forelimb of *C. libidinosus* relative to *C. apella* is hypothesized to be the consequence of terrestrial nut cracking with hammer stones and anvils or increased climbing.

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LITERATURE CITED

Agrawal KR, Lucas PW, Prinz JF. 1997. Mechanical properties of foods responsible for resisting food breakdown in the human mouth. J Dent Res 77:1931–1938.

Altmann SA. 1998. Foraging for Survival: yearling Baboons in Africa. Chicago: University of Chicago Press.

Anapol F, Lee S. 1994. Morphological adaptation to diet in platyrrhine primates. Am J Phys Anthropol 94:239–261.

Ashby MF. 1992. Physical modeling of materials problems. Mater Sci Technol 8:102–111.

Bonner JT. 1965. Size and cycle. Princeton: Princeton University Press.

Bouvier M. 1986a. Biomechanical scaling of mandibular dimensions in New World monkeys. Int J Primatol 7:551–567.

Bouvier M. 1986b. A biomechanical analysis of mandibular scaling in Old World monkeys. Am J Phys Anthropol 69:473–482.

Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge: Belknap Press of Harvard University. p 73–88.

Cole TM. 1992. Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. J Hum Evol 23:253–282.

Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. Int J Primatol 19:971–998.

Constantino P, Wright BW. 2009. The importance of fallback foods in primate ecology and evolution. Am J Phys Anthropol 140:653–660.

Covert HH, Le KQ, Wright BW. 2008. On the brink of extinction: conservation and ecology of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*). In: Fleagle JG, Gilbert CC, editors. Elwyn Simons: a search for origins. New York: Springer Science and Business Media. p 409–427.

Curtis DJ. 2004. Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. Am J Primatol 124:234–247.

Daegling DJ. 1989. Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. Am J Phys Anthropol 80:91–106.

Daegling DJ. 1992. Mandibular morphology and diet in the genus *Cebus*. Int J Primatol 13:545–570.

Daegling DJ. 2002. Bone geometry in cercopithecoid mandibles. Arch Oral Biol 47:315–325.

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

Dias LG, Strier KB. 2003. Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. Int J Primatol 24:209–221.

Doran D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. Int J Primatol 18:183–206.

Fleagle JG, McGraw WS. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. Proc Natl Acad Sci USA 96:1157–1161.

Ford SM, Davis LE. 1992. Systematics and body size: implications for feeding adaptations in New World monkeys. Am J Phys Anthropol 88:415–468.

Ford SM, Hobbs DG. 1996. Species differentiation as seen in the postcranial skeleton of *Cebus*. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. NewYork: Plenum. p 229–249.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, Oliveira M. 2004a. Wild capuchin monkeys use anvils and stone pounding tools. Am J Primatol 64:359–366.

Fragaszy D, Visalberghi E, Fedigan L. 2004b. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Grueter CC, Li D, Ren B, Wei F, Xiang Z, van Schaik CP. 2009. Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. Am J Phys Anthropol 140:700–715.

Gursky S. 2000. Effect of seasonality on the behavior of an insectivorous primate. Tarsius spectrum. Int J Primatol 21:477–495.

Heiduck S. 1997. Food choice in masked titi monkeys (*Callicebus personatus melanochir*): selectivity or opportunism? Int J Primatol 18:487–502.

Hershkovitz P. 1949. Mammals of northern Colombia. Preliminary Report No. 4: monkeys (Primates) with taxonomic revisions of some forms. Proc US Natl Museum 98:323–427.

Hill DA. 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. Am J Primatol 43:305–322.

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

Hylander WL. 1985. Mandibular function and biomechanical stress and scaling. Am Zool 25:315–330.

Hylander WL. 1988. Implications of in vivo experiments for interpreting the functional significance of "robust" australopithecine jaws. In: Grine FE, editor. Evolutionary history of the "Robust" Australopithecines. New York: Aldine de Gruyter. p 55–83.

Hylander WL, Johnson KR. 1994. Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. Am J Phys Anthropol 94:523–547.

Izawa K, Mizuno A. 1977. Palm-fruit cracking behavior of wild black-capped capuchins. Primates 18:773–792.

Jolicoeur P. 1963. The multivariate generalization of the allometry equation. Biometrics 18:497–499.

Jungers WL. 1977. Hind limb and pelvic adaptations to vertical climbing and clinging in *Megaladapis*, a giant subfossil prosimian from Madagascar. Yrbk Phys Anthropol 20:503–524.

Jungers WL, Fleagle JG. 1980. Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. Am J Phys Anthropol 53:471–478.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 38:137–161.

Kay RF. 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141–151.

Kinzey WG. 1974. Ceboid models for the evolution of hominoid dentition. J Hum Evol 3:193–203.

Kinzey WG. 1978. Feeding behavior and molar features in two species of titi monkey. In: Chivers DJ, Herbert J, editors. Recent advances in primatology Vol. 1: Behavior. London: Academic Press. p 373–385.

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee versus cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar P, editor. Evolution of human diet: the known, the unknown, and the unknowable. Oxford: University of Oxford Press. p 324–343.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. The hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am J Phys Anthropol 125:363–368.

Le KQ Nguyen AD, Vu AT, Wright BW, Covert HH. 2006. Diet of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in the Khau Ca area. Ha Giang Province, Northeastern Vietnam. Viet J Primatol 1:75–84.

Leiberman DE. 1996. How and why humans grow thin skulls: experimental evidence for systemic cortical robusticity. Am J Phys Anthropol 101:217–236.

Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. Int J Primatol 14:257–313.

Leighton M, Leighton D. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton SL, Whitmore TC, Chadwick AC, editors. Tropical rain forest: ecology and management. Boston: Blackwell. p181–196.

Liem KF. 1980. Adaptive significance of intra and interspecific differences in the feeding repertoires of cichlid fishes. Am Zool 20:295–314.

Liu Q, Simpson K, Izar P, Ottoni E, Visalberghi E, Fragaszy D. 2009. Kinematics and energetics of nut-cracking in wild capuchins monkeys (*Cebus libidinosus*) in Piauí. Brazil. Am J Phys Anthropol 138:210–220.

Llorens L, Casinos A, Berge C, Majoral M, Jouffroy FK. 2001. A biomechanical study of the long bones in platyrrhines. Folia Primatol 72:201–216.

Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press.

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 72:11–25.

Lucas PW, Prinz JF, Agrawal KR. 2002. Food physics and oral physiology. Food Quality Preferences 13:203–213.

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

Madden M, Hinely AJ, Fragaszy D, Ottoni EB, Izar P, Visalberghi E. 2007. Modelling the monkey habitat in Brazil. Geospat Today 5:26–35.

Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219–1236.

Martins MM, Setz EZF. 2000. Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. Int J Primatol 21:467–476.

Masterson T. 1996. Cranial form in *Cebus*: an ontogenetic analysis of cranial form and sexual dimorphism, Ph.D. dissertation, University of Wisconsin.

Matsumoto-Oda K, Hosaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale mountains. Int J Primatol 19:999–1011.

McFarland-Symington M. 1988. Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park. Peru. Am J Primatol 15:45–67.

Mittermeier RA, van Roosemalen MGM. 1981. Preliminary observations on habitat use and diet in eight Surinam monkeys. Folia Primatol 36:1–39.

Mosimann E. 1970. Size allometry: size and shape variables with characteristics of the log normal and generalized gamma distributions. J Am Stat Assoc 65:930–945.

Mosimann KE, James FC. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. Evolution 33:444–459.

Ottoni EB, Izar P. 2008. Capuchin monkey tool use: overview and implications. Evol Anthropol 17:171–178.

Overdorff DJ, Strait SG, Telo A. 1997. Seasonal variation in activity and diet in a small bodied folivorous primate. Hapalemur griseus, in southeastern Madagascar. Am J Primatol 43:211–223.

Plavcan MJ, Daegling DJ. 2006. Interspecific and intraspecific relationships between tooth size and jaw size in primates. J Hum Evol 51:171–184.

Polk JD, Demes B, Jungers WL, Biknevicius AR, Heinrich RE, Runestad JE. 2000. A comparison of primate, carnivoran, and rodent limb bone cross-sectional properties: are primates really unique? J Hum Evol 39:297–325.

Poulsen JR, Clark CJ, Smith TB. 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. Am J Primatol 54:91–105.

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

Ravosa MJ. 1996. Mandibular form and function in North American and European Adapidae and Omomyidae. J Morph 229:171–190.

Reist JD. 1984. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Can J Zool 63:1429–1439.

Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. Am Natural 151: 223–235.

Rosenberger AL. 1992. Evolution of feeding niches in new world monkeys. Am J Phys Anthropol 88:525–562.

Ruff CB. 1987. Structural allometry of the femur and the tibia in Hominoidea and Macaca. Folia Primatol 48:9–49.

Ruff CB. 2000. Body size, body shape, and long bone strength in modern humans. J Hum Evol 38:269–290.

Ruff C, Holt B, Trinkhaus E. 2006. Who's afraid of the big bad Wolff?: "Wolff's Law" and bone functional adaptation. Am J Phys Anthropol 129:484–498.

Schultz AH. 1953. The relative thickness of the long bones and the vertebrae in primates. Am J Phys Anthropol 11: 277–311.

Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within species diet variability in fossil hominins. Nature 436:693–695.

Sigg H, Stolba A. 1981. Home range and daily march in a Hamadryas baboon troop. Folia Primatol 36:40–75.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–559.

Smith RJ, Petersen CE, Gipe DP. 1983. Size and shape of the mandibular condyle in primates. J Morph 177:59–68.

Sokal R, Rohlf FJ. 1995. Biometry. New York: W.H. Freeman.

Stock JT, Shaw CN. 2007. Which measures of diaphyseal robusticity are robust? A comparison of external methods of quantifying the strength of long bone diaphysis to cross-sectional geometric properties. Am J Phys Anthropol 134:412–423.

Struhsaker T, Leland L. 1977. Palm nut smashing by *Cebus a. apella* in Colombia. Biotropica 9:124–126.

Taylor AB. 2002. Masticatory form and function in African apes. Am J Phys Anthropol 117:133–156.

Terborgh J. 1983. Five new world primates. Princeton: Princeton University Press.

Tutin CE, Ham RM, White LJ, Harrison MJ. 1997. The primate community of the Lopé Reserve. Gabon: diets, responses to fruit scarcity, and effects on biomass. Am J Primatol 42:1–24.

van Roosmalen MGM. 1980. Habitat preferences, diet, feeding behavior, and social organization of the black spider monkey, *Ateles paniscus paniscus* in Surinam. Ph.D. dissertation, University of Wageningen, The Netherlands.

Vincent JFV. 1992. Biomechanics, materials: a practical approach. Oxford: Oxford University Press.

Vinyard CJ, Ryan TM. 2006. Cross-sectional bone distribution in the mandibles of gouging and non-gouging platyrrhines. Int J Primatol 27:1461–1490.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. Am J Phys Anthropol 120:153–170.

Visalberghi E, Fragaszy D, Izar P, Ottoni EB. 2005. Terrestriality and tool use. Science 318:951.

Visalberghi E, Fragaszy D, Ottoni EB, Izar P, Oliveira MG, Andrade FRD. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. Am J Phys Anthropol 132:426–444.

Wallace RB. 2005. Seasonal variations in diet and foraging behavior of Ateles chamek in a southern Amazonian tropical forest. Int J Primatol 26:1053–1075.

Watts DP. 1998. Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). Int J Primatol 19:929–948.

White FJ. 1998. Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. Int J Primatol 19:1013–1027.

Williams S, Wright BW, Truong VD, Vinyard CJ. 2005. The mechanical properties of foods used in experimental studies of primate masticatory function. Am J Primatol 67:329–346.

Worman CO, Chapman CA. 2005. Seasonal variation in a tropical ripe fruit quality and the response of three frugivores. J Trop Ecol 21:689–697.

Wright BW. 2004. Ecological distinctions in diet, food toughness and masticatory anatomy in a community of six neotropical primates in Guyana, South America. Ph.D. dissertation. University of Illinois, Urbana Champaign.

Wright BW. 2005a. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473–492.

Wright KW. 2005b. Interspecific and ontogenetic variation in locomotor behavior, habitat use, and postcranial morphology in *Cebus apella* and *Cebus olivaceus*. Ph.D. dissertation, Northwestern University.

Wright KW. 2007. The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. Am J Primatol 69:1–21.

Yamagiwa J. 2009. Fallback foods and dietary partitioning among Pan and Gorilla. Am J Phys Anthropol 140:739–750.

Yamakoshi G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. Am J Primatol 106:283–295.