Chapter 11
Mechanical and Nutritional Properties of Food as Factors in Platyrrhine Dietary Adaptations

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11.1 Introduction

Platyrrhines face a vast array of potential food resources in the Neotropics. Ecological challenges associated with finding, ingesting, masticating, and digesting foods are influenced by food availability and accessibility. Food availability is influenced by seasonal variation in forest productivity, fruiting synchrony, and crop size (e.g., Stevenson 2001; Chapman et al. 2003, but *see* Milton et al. 2005). Accessibility, on the other hand, is related to such factors as fruit and seed size, the ability to breach mechanically challenging tissues, to tolerate secondary chemical compounds, and to balance nutrient intake. Our goal in this chapter is to examine the diversity of platyrrhine responses to this second variable – gaining access to and processing foods.

All platyrrhine genera include fruit in their diets, but the annual percentage of fruit intake ranges widely from 8% in *Cebuella* to 86% in *Ateles* (Table 11.1). A wide variety of other resources including exudates, fungi, leaves, flowers, nectar and insect or vertebrate prey make up the balance, or at times the bulk, of annual diets. Some particularly interesting feeding behaviors seen in platyrrhines signal the evolution of specific adaptations. These include the ability to extract and digest plant resources such as gums by *Cebuella* and *Callithrix* (Nash 1986; Power and Oftedal 1996), fungi by *Callimico* (Porter 2001; Porter and Garber 2004; Hanson et al. 2006; Rehg 2006), and seeds by the pitheciins (van Roosmalen et al. 1988; Ayres 1989; Kinzey and Norconk 1990; Kinzey 1992; Peetz 2001; Norconk and Conklin-Brittain 2004). Although gums, seeds and fungi are ingested by other primate species [especially lemurs (Nash 1989; Hemingway 1998) and colobines (Waterman and Kool 1994; Kirkpatrick 1998)], they are used very intensively by these platyrrhines, composing either a majority of their diet during a single season, a subset of the annual diet, or are routinely and extensively used throughout the year.

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Table 11.1 Average annual percentages of plant parts and insects in the diets of 16 platyrrhine genera

Primate genus	Exudates (%)	Arils (%)	Fungi (%)	Fruit pulp (%)	Flowers (%)	Seeds (%)	Whole fruit (%)	Young leaves (%)	Mature leaves (%)	Insects (%)
Cebuella	60			8						30
Callithrix	45			16						39
Leontopithecus	9			53	7					25
Saguinus	10			35				3		45
Callimico	1		29	29						41
Saimiri				25	5			10		60
Cebus				47		8		8		33
Aotus				45	14			41		
Callicebus				59	4	27		6		4
Pithecia		2		16	2	61	11	5		3
Cacajao				18	6	67				
Chiropotes				42	1	51				4
Alouatta				34	9			38	16	
Lagothrix				64	4	1	8	6		9
Brachyteles				27	11	5		42	9	
Ateles				86	3			11		

Sources for dietary data: Ayres 1986; Strier 1991; Norconk 1996; Palacios et al. 1997; Peetz 2001; Porter 2001; NRC 2003; Di Fiore 2004; Wallace 2005. Species listed by body size from small to large. These data are composites for each genus and do not necessarily equal 100%.

Although considerable work has been done on platyrrhine feeding strategies, we plan to further examine these food accessibility issues taking a slightly different approach. We devised three variables that could be compared among 16 genera of platyrrhines. Each of the variables was compiled from both field and laboratory studies and each represents considerable built-in complexity. The three variables are (1) the morphology of the masticatory apparatus, (2) the mechanical protection of plant foods opened or ingested by platyrrhines, and (3) the nutrient composition of foods ingested and dietary intake in the form of metabolizable energy. We approach this chapter from diverse backgrounds and hope that by combining our efforts we will contribute to a more comprehensive understanding of the dietary strategies of the modern platyrrhine radiation.

11.2 General Characteristics of Platyrrhine Diets

Platyrrhines provide a nice test of Kay's body mass threshold model. All of them are frugivores to some extent, thus one would expect to find a shift between higher proportions of protein-rich insects to leaves at one kilogram of body mass (Kay 1984). Most of the smallest-bodied platyrrhines balance diets of exudates with fruit and insects and fit the model well with *Callimico* unique in its dietary combination of insects with fruit and fungi (Porter 2001). The percentage of insects in the diet is much reduced in larger-bodied platyrrhines ($< 10\%$) and the ateline diets are relatively high in their leaf portions. However, two platyrrhine genera do not appear to fit Kay's model. *Cebus* spp. have a higher intake and *Aotus* spp. have a lower intake of insects than expected, based on their body mass. The well-known extractive foraging strategy of *Cebus* enhances their reliability of access to protein-rich animal prey (e.g., Fragaszy 1986; Janson and Boinski 1992). The explanation for the low intake of insects in *Aotus* spp. is perhaps related to the inability to quantify insect eating in this nocturnal primate (Fernandez-Duque 2007). Seeds predominate in the diets of the saki-uacari group (pitheciines) and are a relatively rarely used resource among the rest of the platyrrhines. In the sakis and uacaris, various categories of fruit (e.g., fruit pulp, seeds, and whole fruit) make up more than 75% of the diet. Ultimately, a revision of Kay's model may be necessary as more nutritional data are collected to include better documentation of protein levels in wild foods and wild primate diets. Kay (1984) suggested that a dietary shift occurred along a continuum of body mass in primates – from protein derived from insects in primates weighing less than 1kg to protein derived from leaves in larger primates. Nutritional studies suggest that protein is both a ubiquitous resource in tropical plants, and an unpredictable one – particularly for fruit. Fruit pulp is often found to be relatively low in protein (e.g., 9.5%) (on the basis of dry matter, DM) compared to the average for leaves (22% DM) (Conklin-Brittain et al. 1998: Table III), but not always. *Capparis muco* fruit pulp eaten by white-faced sakis is 18.7% (DM) crude protein (Norconk and Conklin-Brittain 2004: Table I), but at this point we do not know if this is a relatively common or a rare occurrence. With the incorporation of other variables, such as longer termed studies and nutritional data, we will inevitably expand the limited dimensionality of Kay's original paradigm.

11.3 Materials and Methods: Our Approach in this Chapter

We begin our examination of how the diversity of platyrrhine feeding strategies relates to accessing and processing foods by reviewing variation in platyrrhine masticatory apparatus form, dietary mechanical properties, digestion and nutrient intake. Following these reviews, we attempt to integrate summary data from each review to explore potential interrelationships. Finally, we highlight where future research can further our understanding of how platyrrhines access and process selected resources.

11.3.1 Morphometric Sample of the Masticatory Apparatus

In order to review masticatory apparatus functional morphology, morphometric data on platyrrhine skulls were compiled from either unpublished measurements taken on museum specimens or from published species means. For the unpublished museum data, wild-shot individuals were sampled preferentially. These measurements were either taken with calipers or from video analysis following the methods outlined in Spencer and Spencer (1995).

11.3.2 Food Properties Sample

The review of feeding ecology and food mechanics are based primarily on data collected at Turtle Mountain in the Iwokrama reserve in central Guyana, South America from October 1999 to December 2000 (Wright 2004). Plant tissues were categorized as: fruit mesocarp, epicarp, seed coat (or endocarp), exocarp-mesocarp (adhering epicarp-mesocarp), endosperm, pod, seed (whole), fruit (whole), leaf (leaf lamina), spadix (spathes and fruiting spadices of aroid epiphytes), stem (of flowers & leaves), petal (of flowers), flower reproductive (non-petal or stem flower parts), gum (exudate) or aril following van Roosmalen (1984). Detailed feeding data were recorded when possible with particular attention paid to the sequence of oral/manual food processing. The position of the food along the dental arcade was also recorded when detailed observations could be made and the frequency of distinct processing techniques and sequences was calculated.

While in the field, samples of food tissues were collected and their fracture toughness was measured. The portable universal tester used in the field was designed specifically for testing the physical properties of foods processed by primates (Darvell et al. 1996; Lucas et al. 2001), and its use is well established in field studies of primate dietary ecology.

11.3.3 Nutritional Sample

The nutritional sample was drawn from several sources. (1) Fifty-seven plant species collected from Lago Guri, Venezuela, from 1991 to 1995 during long-term studies of *Pithecia pithecia* and *Chiropotes satanas* (Kinzey and Norconk 1993; Norconk 1996; Norconk and Conklin-Brittain 2004; unpublished data). (*See* Norconk and Conklin-Brittain 2004 for methods used in the nutritional analysis). Additional smaller data sets were also compiled for sympatric primates, *Alouatta seniculus*, and *Cebus olivaceus* in Lago Guri. (2) Fifty-five plant species, including both leaves and fruits, collected in Belize (Silver et al. 2000), during a thesis project studying the diet of black howler monkeys (*Alouatta pigra*). (3) Forty-five plant species also collected in Venezuela (Castellanos and Chanin 1996), for a study of spider monkey (*Ateles belzebuth*) fruits and arils. (4) Sixteen plant species, mainly fruits, and two insects from Isla Barro Colorado in Panama (Hladik et al. 1971). (5). Parts of several smaller datasets, especially for flowers, exudates, fungi, and insects (Gaulin and Craker 1979; Nash 1984; Garber 1988; Brown and Zunino 1990; Oftedal 1991; Smith 2000; Hanson et al. 2006).

Using this nutritional sample, we generated an estimated metabolizable energy density (kcal/100 g of diet dry weight) for each major food source by first computing total nonstructural carbohydrates *(TNC) = 100 – % insoluble fiber – % lipids – % protein – % ash*. Estimated metabolizable energy (ME) was calculated using the commonly used physiological fuel values of 4 kcal/g for carbohydrates (TNC) and protein, and 9 kcal/g for lipids (NRC 2003; Conklin-Brittain et al. 2006). We estimated metabolizable energy density for the diets of 16 platyrrhine genera, ranked the genera from highest to lowest and compared that to their body weights. Empirically determined ME, where energy lost through feces, urine, and respiration is subtracted from energy gained by intake, is more accurate, but this method has been used for very few wild primates (Altmann 1998; Conklin-Brittain et al. 2006; Miller et al. 2006).

11.4 Mechanical Assessment of Platyrrhine Masticatory Apparatus Form

The masticatory apparatus becomes involved in the feeding process as foods are brought into the mouth and mechanically reduced before being passed into the rest of the gastrointestinal tract for nutrient extraction. For the part of this process involving the masticatory apparatus, feeding can be somewhat arbitrarily broken down into ingestion, followed by mastication, and finally swallowing (Hiiemae 2000).

Ingestion involves using the teeth to forcibly extract and/or separate potential foods for subsequent chewing (Hiiemae and Crompton 1985). Ingestion may be the most variable of these three processes as it can pose minimal to significant mechanical challenges to an animal. Ingestive activities have been variably described as incision, harvesting, biting, husking, cropping, gouging, tearing, breaching, scraping and/or piercing in South American primates (Eaglen 1986; Rosenberger 1992; Anapol and Lee 1994; Vinyard et al. 2003; Wright 2005). After bringing a bite-sized piece of food into the mouth, chewing or mastication begins. Chewing typically involves consecutive, rhythmic patterns of jaw movement and loading during which foods are mechanically broken down between the upper and lower postcanine teeth (Hiiemae 1978). Swallowing is the most coordinated and likely stereotypical of these three processes. We do not consider swallowing in this chapter.

The mechanical demands placed on the masticatory apparatus during ingestion and mastication are broadly divisible into those related to force production and dissipation versus those associated with moving the jaw and tongue. While the forces generated at the bite point are paramount to successful food breakdown, the ability to efficiently produce these bite forces and successfully resist internal loads in the skull during feeding also impact the form of the platyrrhine masticatory apparatus. Most functional analyses of masticatory apparatus form among platyrrhines focus on the generation of these external bite forces and the dissipation of the resulting internal loads (Bouvier 1986a; Daegling 1992; Anapol and Lee 1994; Wright 2005). Research on jaw and tongue movements during feeding (Vinyard et al. 2003) lags behind functional studies of the force-related demands on the platyrrhine masticatory apparatus.

The structural and mechanical properties of an animal's diet as well as how it chooses to manipulate this diet must be fundamentally linked to the mechanical demands placed on the masticatory apparatus during ingestion and mastication. This overarching conclusion is bolstered by observations that the range of jaw movements and magnitude of jaw loads during chewing are influenced by these structural and mechanical properties as well the relative position of a chewing cycle in a chewing sequence (Hiiemae and Kay 1973; Luschei and Goodwin 1974; Hiiemae 1978; Hylander 1979a; Hylander et al. 1987, 2000; Chew et al. 1988; Agrawal et al. 1998; Vinyard et al. 2006). Thus, we should expect any relationship between function and masticatory apparatus form to be predicated on dietary properties and feeding behavior. Our goal for the remainder of this section is to examine the functional consequences of variation in masticatory apparatus form among platyrrhines.

11.4.1 Jaw Forms Linked to Force Production

We can initially approximate a bite force anywhere along the tooth row using a static beam model in either a sagittal or frontal view (e.g., Hylander 1975; Smith 1978). In sagittal projection, bite force can be estimated as:

$$\text{Bite force(Fb)} = (muscle\ moment\ arm(IN) * muscle\ force(Fm))/bite\ point\ load\ arm(OUT)$$

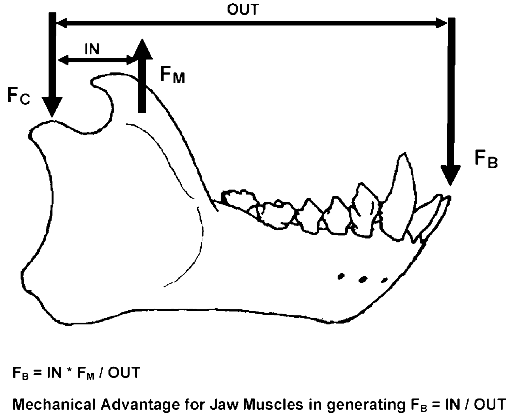

Fig. 11.1 A static beam model of vertical bite force at the incisors. The mechanical advantage of the jaw-closing muscles is estimated as the ratio of the perpendicular distance from the line of action of the jaw-closing muscle (arrow labeled F_m) to the temporomandibular joint (IN-lever) divided by the distance from the joint to the incisal bite point (OUT-lever). The sum of the vertical force created by the jaw-closing muscles is represented by F_m. (The location of the jaw-closing muscle line of action is arbitrarily placed for the purpose of illustration). Abbreviations: $F_m =$ vertical force generated by the jaw-closing muscles, $F_b =$ vertical bite force, $F_c =$ vertical reaction force at the condyle, IN = the in-lever or moment arm for the jaw-closing muscles and OUT = the out-lever or load arm for biting at the incisors

(Fig. 11.1). This static bite force estimate is divisible into the force generated by the combined contraction of the jaw adductors (Fm) and a leverage component describing the mechanical advantage (IN/OUT) of the muscle (IN) and bite point (OUT) moment arms. Morphological changes affecting either of these components may influence an animal's ability to generate bite force during ingestion or mastication. Unfortunately, we know next to nothing about variation in bite forces among platyrrhines.

One reason we know so little about bite forces in platyrrhines is that we lack a comprehensive functional analysis of their jaw-closing muscles. The existing information on platyrrhine jaw muscles focuses on descriptive morphology (e.g., Ross 1995) or descriptions combined with muscle weights (Starck 1933; Schumacher 1961; Turnbull 1970; Cachel 1979). Taylor and Vinyard (2004) provide the only functional analysis of jaw-muscle architecture in platyrrhines. They compared masseter architecture in gouging and non-gouging callitrichines, but lacked the taxonomic breadth to be informative across platyrrhines. Based on the limited data available at the time, Bouvier and Tsang (1990) suggested that platyrrhines do not differ markedly from catarrhines in their relative jaw-muscle configurations.

In contrast to data on muscle architecture, we know more about how variation in skull form impacts the mechanical advantage of the platyrrhine masticatory apparatus. Most recently, Wright (2005) compared mechanical advantage for the jaw-closing muscles at the incisors, canines and M_2s across ten platyrrhine species. This analysis focused on *Cebus* spp. finding that they tended to exhibit the highest mechanical advantage for the jaw-closing muscles with the exception of the medial pterygoid. *Chiropotes satanas* tended to exhibit the next highest mechanical advantage followed by *Pithecia pithecia*, *Lagothrix lagotricha* and *Ateles paniscus*. *Alouatta seniculus, Callicebus* spp. and *Aotus trivirgatus* exhibited the least mechanical advantage among these species. Anapol and Lee (1994) estimated masseter and temporalis lever arms for eight platyrrhines. Their analysis focused more on variation among lever arm lengths noting that the masseter lever arm showed relatively less variation than the temporalis lever arm.

11.4.2 Jaw Forms Linked to Force Production: A Reanalysis

We can extend these previous analyses of jaw-muscle mechanical advantage by both adding species and incorporating an estimate of the relative force contributed by each of the three main jaw-closing muscles. We measured moment arms for the temporalis, masseter and medial pterygoid, similar to Wright (2005), for 22 platyrrhine species. We then scaled these moment arms by the percentage of the total jaw-adductor muscle weight each muscle represents based on the platyrrhines ($n = 4$) measured by Turnbull (1970). Individual moment arms as well as the average moment arm scale close to or slightly below isometry relative to incisor, canine and molar biting moment arms (Table 11.2). Similar scaling patterns are observed when regressed on body mass. The only scaling comparison to deviate from isometry is the negative allometry of the masseter and average muscle moment arm relative to biting at M^1.

Relative mechanical advantage among platyrrhine species trends toward a size-related decrease in biting leverage, particularly for biting along the postcanine dentition (but see Pirie 1976). Figure 11.2 shows that smaller platyrrhines tend to have greater mechanical advantage on average than larger species for biting at M_1 ($r = -0.57$; $P = 0.006$). A similar, but weaker, trend is observed in an analogous comparison for biting at the incisors ($r = -0.41$; $P = 0.06$). A size-related trend is not observed for biting at the canines ($r = -0.23$; $P = 0.29$). These size-correlated trends appear strongest in callitrichines; although, it is unclear if this pattern is directly related to masticatory or ingestive functions in this group. In summary, larger platyrrhines may start out with a size-correlated disadvantage for producing bite forces during mastication or ingestion.

Superimposed on this size-related trend are several differences in mechanical advantage that correlate with variation in diet. Among the non-callitrichines, *Cebus apella* possesses the highest leverage for biting at M_1 (Fig. 11.2) as well as the canines and incisors (data not shown). *Chiropotes satanas* and *Cacajao melanocephalus* have the next highest advantage for M_1 biting followed by *Pithecia pithecia* and *Cebus albifrons*. These results support previous observations that these “hard-object” feeders tend to have relatively greater mechanical advantage (Anapol and Lee 1994; Wright 2005), particularly during anterior tooth use. After the pitheciines and *Cebus* spp., there are a group of primates with intermediate mechanical

Table 11.2 Scaling of moment arms for the jaw-closing muscles versus biting load arms and body mass among platyrrhines

	Incisor Load Arm		Canine Load Arm		M_1 Load Arm		Body Mass$^{1/3}$	
Jaw-Muscle Moment Arm[1]	LS/RMA Slope (95% CI)[2]	R[3]	LS/RMA Slope (95% CI)	R	LS/RMA Slope (95% CI)	R	LS/RMA Slope (95% CI)	R
Temporalis	0.98 (±0.117)	0.969	1.00 (±0.120)	0.968	0.94 (±0.117)	0.966	0.98 (±0.213)	0.906
	1.01 (±0.117)		1.03 (±0.120)		0.97 (±0.117)		1.08 (±0.213)	
Masseter	0.96 (±0.055)	0.992	0.97 (±0.057)	0.992	0.91 (±0.069)	0.987	0.97 (±0.153)	0.947
	0.97 (±0.055)		0.98 (±0.057)		0.92 (±0.069)		1.02 (±0.153)	
Medial Pterygoid	0.92 (±0.123)	0.962	0.94 (±0.126)	0.961	0.88 (±0.117)	0.957	0.90 (±0.225)	0.883
	0.96 (±0.123)		0.98 (±0.126)		0.92 (±0.125)		1.02 (±0.225)	
Scaled Jaw-Muscle Average[4]	0.96 (±0.043)	0.995	0.98 (±0.046)	0.995	0.92 (±0.057)	0.991	0.90 (±0.225)	0.883
	0.96 (±0.043)		0.98 (±0.046)		0.93 (±0.057)		1.02 (±0.225)	

[1] All regressions and correlations are based on 22 species' means (n = 22). (see Fig. 11.1 for measurement and species' descriptions).

[2] Top line is least-squares regression (LS) of a muscle moment arm on a moment arm for various bite points. Bottom line is reduced-major axis regression (RMA). The 95% confidence interval for the slope estimate is in parentheses. All regressions are significant $\alpha = 0.05$.

[3] Pearson's product moment correlation. All correlations are significant $\alpha = 0.05$.

[4] Calculated as average of the three muscle moment arm after taking into account relative percentage of total jaw-adductor mass across platyrrhines. [= (*Temporalis**0.52 + *masseter**0.33 + *medial pterygoid**0.17)/3].

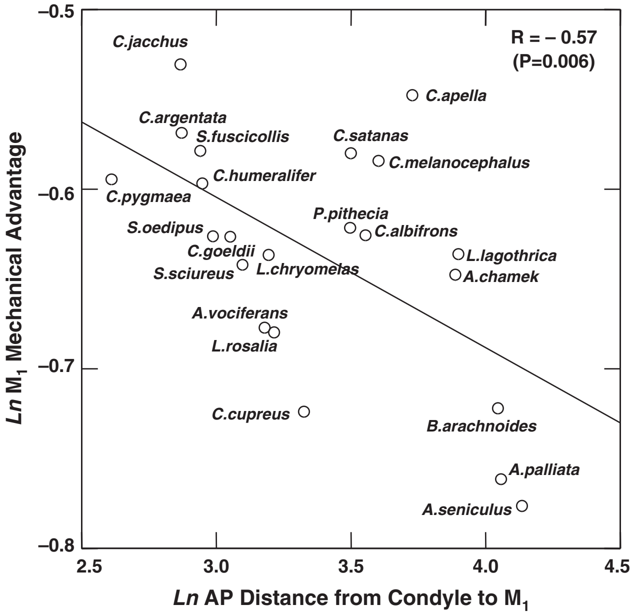

Fig. 11.2 Plot of mechanical advantage for biting at M_1 versus the distance from the condyle to M_1 among platyrrhines. M_1 mechanical advantage is estimated as: *((TempMA*0.52)+(MassMA*0.31)+(MedPtery*0.17))/Condyle-*M_1 *distance*. TempMA is measured as the distance from the back of the condyle to the tip of the coronoid process. MassMA is the distance from the back of the glenoid fossa to the tip of the anterior attachment of the masseter at the root of the zygoma. MedPtery is the AP distance from the back of the glenoid to the midline of the pterygoid plates. Each of these muscle moment arms is multiplied by the relative percentage that muscle contributes to overall jaw-adductor weight in four platyrrhines measured by Turnbull (1970). This scaling provides an initial estimate of relative force contribution, based on weight, from each of the jaw-closing muscles. Condyle-M_1 is the AP distance from the back of the glenoid to M_1

leverage that are classically described as "frugivorous." More folivorous species, such as *Alouatta palliata*, *A. seniculus* and to a lesser extent *B. arachnoides*, show the lowest mechanical advantage for M_1 biting (Wright 2005). In contrast to the relatively higher leverage in *Cebus* spp. and pitheciines, leverage improvement is not related to folivory in platyrrhines. It is interesting to speculate based on these observations that while breaking down pliant, tough leaves may require significant mechanical work at the molars, manifested as repetitive crack propagation, it may not necessarily involve generating extremely high bite forces during chewing.

11.4.3 Jaw Forms Linked to Load Resistance

The platyrrhine masticatory apparatus likely experiences its largest internal loads during the power strokes of incision and mastication when foods are mechanically fractured and/or reduced. The morphological bottom line for resisting these loads is that bigger is better. In some cases, bigger in a certain direction (i.e., a specific shape) provides improved load resistance ability. In other situations, larger in magnitude regardless of direction, offers increased load resistance. Previous in vivo analyses of living primates indicate that the mandibular condyles, corpora and symphyses resist significant loads during mastication and ingestion (e.g., Hylander 1979a,b, 1984, 1985; Hylander et al. 1987, 1998).

Multiple studies have translated Hylander's in vivo strain data into expected morphological differences among platyrrhines that differ in diet and/or feeding behavior. We can summarize the morphological variation in load resistance ability across platyrrhines by combining shape measures (i.e., shape ratios) of the mandibular condyle, corpus and symphysis in a multivariate principal components analysis (PCA) (Table 11.3; Fig. 11.3). The first component of this PCA explains approximately 52% of the variation in these length and width shapes among platyrrhines. Furthermore, all variables have positive loadings suggesting that this component can be initially interpreted as a jaw robusticity factor. With the exception of anterior-posterior condyle length, each variable is significantly correlated with its first component score suggesting that most of these shape measures are contributing to this linear estimate of jaw robusticity.

C. satanas and *C. melanocephalus* have the largest scores along the first component suggesting these taxa have relatively robust mandibles linked to their ingesting mechanically challenging seeds (e.g., Bouvier 1986a; Anapol and Lee 1994; Kinzey 1992; but see Marriog et al. 2004) (Fig. 11.3). The two *Cebus* species have the next highest scores supporting earlier work that members of this genus have relatively robust jaws (Kinzey 1974; Bouvier 1986a; Cole 1992; Daegling 1992;

Table 11.3 Principal components analysis (PCA) for shapes related to load resistance in platyrrhine mandibles[1]

Shape Variable[2]	Component 1[3]	Component 2	Component 3	Component 4
Corpus Depth	0.439/**0.78**	0.246/0.29	0.495/0.39	−0.485/−0.34
Corpus Width	0.449/**0.80**	−0.022/−0.03	−0.564/−0.44	−0.442/−0.31
Symphysis Length	0.467/**0.83**	0.072/0.08	0.046/0.04	0.741/**0.52**
Symphysis Width	0.361/**0.64**	−0.538/−0.62	−0.366/−0.29	0.060/0.04
Condyle Length	0.102/0.18	−0.752/−0.87	0.515/0.41	−0.079/−0.06
Condyle Width	0.498/**0.88**	0.279/0.32	0.189/0.15	0.104/0.07
Eigenvalues[4]	3.14/52.3%	1.35/22.4%	0.62/10.3%	0.49/8.2%

[1] PCA was performed on the correlation matrix for shape variables. Corpus depth (SI) and breadth (ML) are measured at M_1. Symphysis length (primarily SI) and width (AP) are measured following Hylander (1985). Condyle length (AP) and width (ML) are measured from the articular surface of the joint.

[2] Shape variables were created by dividing each measure by the distance from the condyle to M_1.

[3] The first value represents the eigenvectors for each component. The second value is the correlation between the original variable and its component score. Bold correlations are significant at $\alpha = 0.05$.

[4] Eigenvalues are reported first followed by the percentage of total variation explained by that component.

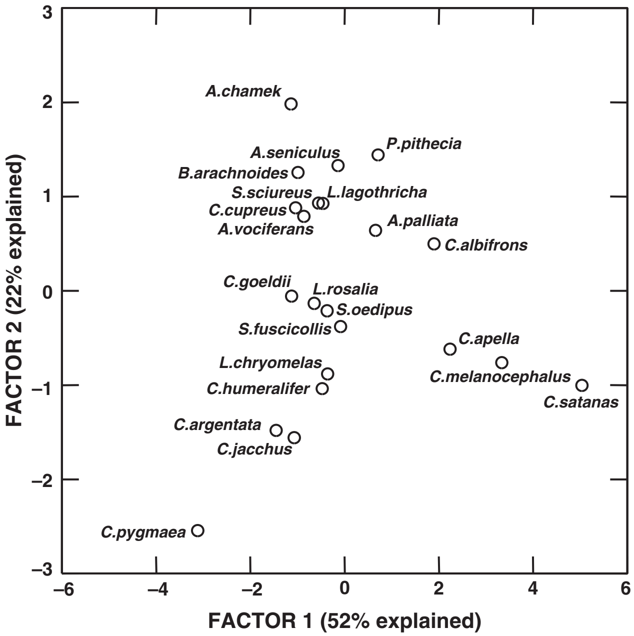

Fig. 11.3 Plot of factors one and two for principal components analysis (PCA) of mandibular shapes across 22 platyrrhine species. See Table 11.3 for descriptions of measurements

Anapol and Lee 1994; Wright 2005). The third pitheciine, *P. pithecia*, and the two folivorous *Alouatta* species are intermediate between these robust forms and the remaining platyrrhine species. The position of *P. pithecia* supports arguments that it is the less robust member of this seed-eating clade (Kinzey 1992; Anapol and Lee 1994). We can hypothesize based on the position of *Alouatta* along this component that folivory is correlated with modest jaw robusticity among platyrrhines. The left half of component one is occupied by the remaining primarily frugivorous, insectivorous and/or gummivorous platyrrhines. The tree-gouging marmosets (i.e., *Callithrix* and *Cebuella*) have relatively gracile jaws among these platyrrhines (Vinyard et al. 2003; Vinyard and Ryan 2006) suggesting that this behavior may not involve relatively large bite forces.

Variation along the second component is primarily contrasting differences in a-p condylar and symphyseal length shapes among platyrrhines. The tree-gouging marmosets along with *C. apella, C. melanocephalus* and *C. satanas* possess relatively elongated condyles and symphyses. Previous morphological analyses suggest that anteroposterior condyle length may be more important in facilitating jaw opening ability (i.e., wide gapes) or load resistance at wide gapes (Smith et al. 1983; Bouvier 1986a,b; Vinyard et al. 2003). If a-p condyle length is unrelated to loads or related to load resistance only in this specific mechanical context, then this might help explain its lack of strong contribution to component one and emphasis in component two. Vinyard et al. (2003) suggest that marmosets have several morphological features of their masticatory apparatus, including anteroposteriorly elongated condyles (a measure directly correlated with curvature and hence rotational ability) that facilitate wide jaw gapes during gouging. Similar work has not been done in pitheciines. We also speculate that the elongated symphyses of these taxa may relate to both improved load resistance ability (e.g., Bouvier 1986a) as well as the need to house the enlarged and procumbent anterior teeth possessed by several of these taxa.

11.4.4 Dental Morphology Linked to Feeding

The teeth play a pivotal role in the mechanics of food breakdown as they provide the points of contact between the masticatory apparatus and foods. Thus, the shape of these contacts (i.e., occlusal morphology) and their spatial distribution (related to tooth size) fundamentally affect how foods break down during feeding. It is not surprising then that primatologists have paid considerable attention to the teeth in functional studies linking platyrrhine masticatory apparatus form to feeding behaviors (Zingeser 1973; Kinzey 1974, 1992; Kay 1975; Rosenberger and Kinzey 1976; Hershkovitz 1977; Rosenberger 1978, 1992; Eaglen 1984; Teaford 1985; Greenfield 1992; Martin et al. 2003; Spencer 2003; Wright 2005). This is an extensive body of work and we provide only a synopsis here.

11.4.5 Postcanine Teeth – Chewing

We can initially, albeit imperfectly, divide the toothrow into the postcanine versus anterior teeth based on basic functional roles. The postcanine teeth, particularly the molars, are used in food reduction during chewing, while the anterior teeth are typically employed during ingestion of food bites. Relative molar areas for 16 platyrrhine genera show *Ateles* and several predominantly fruit-eating/insect-eating callitrichines have relatively small molar areas compared to more leaf-eating and seed-eating platyrrhines (Fig. 11.4) (Zingeser 1973; Pirie 1978; Kanazawa and Rosenberger 1989; Rosenberger 1992; Anapol and Lee 1994). The dedicated seed eaters, *Chiropotes* and *Cacajao*, are intermediate in relative molar area (Fig. 11.4), while *Pithecia* exhibits relatively larger molar areas than these two seed predators (Anapol and Lee 1994). The relatively large molar areas of *Cebus* support interpretation that these species ingest and masticate relatively hard and tough foods (Anapol and Lee 1994; Wright 2005). *Callicebus* has the largest relative molar areas among platyrrhines (Fig. 11.4).

Lucas (2004) develops an excellent series of arguments linking molar occlusal morphology to mechanical properties of foods. In short, fruit eaters are hypothesized to have relatively rounded cusps providing broad opposing surfaces for bursting the cell walls of small packets of fruit flesh. Primary leaf eaters are expected to have opposing blades on upper and lower occlusal surfaces that assist in propagating cracks through tough, flat leaves. Insect eaters are predicted to have sharp blades on

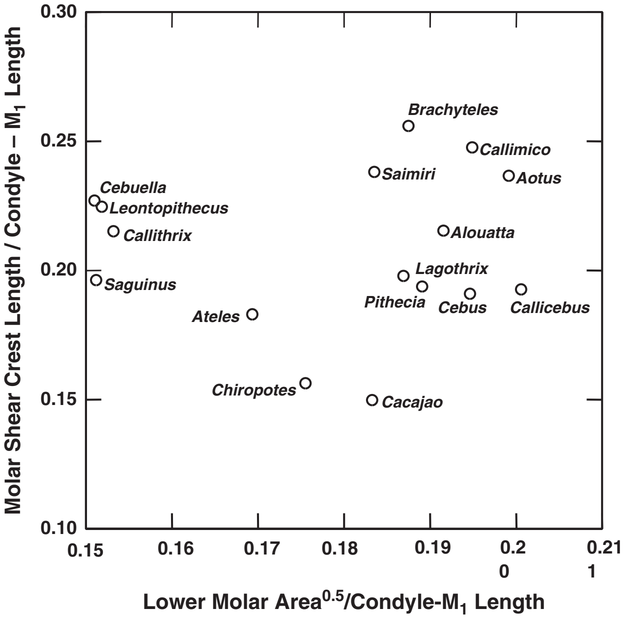

Fig. 11.4 Plot of lower molar area shape versus M_1 shearing crest length shape across 16 platyrrhine genera. Both measures were divided by an estimate of the chewing load arm to create mechanical shape variables. Lower molar area is the sum of individual molar area estimates (length x width) for M_1 – M_3 (M_1 and M_2 in callitrichids lacking an M_3). Molar area data are from Kanazawa and Rosenberger (1989), Rosenberger (1992) and Lucas et al. (1986). Molar shearing crest length is estimated as the sum of 6 shearing crest lengths on the M_1 based on data from Anthony and Kay (1993) and Meldrum and Kay (1997). Descriptions of the measured crests are provided in Kay (1977). To increase the number of platyrrhines represented in this plot, species data were averaged at the genus level. Thus, some generic estimates include different measures from separate species. As such, these comparisons only provide a first-approximation of platyrrhine interrelationships and should be used as preliminary evidence for future comparisons among species

their occlusal surfaces to aid in propagating cracks through cuticle. Seed predators should have rounded cusps that fit in opposing basins providing a mortar and pestle effect on these stress-resistant food items.

One simple way of summarizing occlusal morphology compares relative lengths of “shearing” crests along the molar occlusal surface; a technique developed by Kay and colleagues (Kay 1977; Kay and Covert 1984; Covert 1986; Anthony and Kay 1993; Meldrum and Kay 1997; Kirk and Simons 2001). Species consuming large percentages of leaves and insects should have relatively higher values and hence more blade-like crests, while more frugivorous and gramnivorous species should have lower values linked to more rounded cusps (Kay 1975; Lucas 2004). Using previously published data (Anthony and Kay 1993; Meldrum and Kay 1997), the seed predators *Cacajao* and *Chiropotes* along with the highly frugivorous *Ateles*, exhibit the least developed shearing crests relative to M_1 moment arm length (Kinzey 1992; Rosenberger 1992) (Fig. 11.4). Alternatively, the folivorous *Brachyteles* exhibits the most developed shearing crest lengths (Zingeser 1973).

Alouatta while having relatively longer crests than most genera (Rosenberger and Kinzey 1976), does not exhibit an extreme degree of cresting among platyrrhines. This underlines the generalist nature and broad dietary capabilities of howlers (Milton 1980; Kinzey 1997; Di Fiore and Campbell 2007). Similarly, the frugivorous *Lagothrix* and hard-object feeding *Pithecia* and *Cebus* only show moderately less cresting than many platyrrhines.

11.4.6 Anterior Teeth – Ingestion

Platyrrhines use their incisors and canines in as wide a range of ingestive behaviors as any primate clade. Thus, it is not surprising to see a broad range of platyrrhine anterior tooth morphologies (Rosenberger 1992) linked to this behavioral diversity. Rosenberger (1992) provides an excellent, detailed review of the functional morphology of platyrrhine anterior teeth. We rely heavily on this review. Rosenberger (1992) demonstrates that pitheciines have tall, mediolaterally (ml) narrowed and buccolingually (bl) broad lower incisors and robust canines that facilitates whittling down or reducing the exocarp and harvesting seeds from hard and tough fruit pericarps (Kinzey and Norconk 1990; Kinzey 1992; Rosenberger 1992; Anapol and Lee 1994) Tree-gouging marmosets, *Callithrix* and *Cebuella*, have modified their lower anterior teeth to form a sharp wedge facilitating their biting into tree barks to elicit exudate flow (Coimbra-Filho and Mittermeier 1977; Rosenberger 1978, 1983, 1992; Sussman and Kinzey 1984; Nash 1986; Garber 1992; Natori and Shigehara 1992). *Cebus apella* tends to have robust anterior teeth linked to aggressive ingestion of a broad range of potential foods including hard and tough objects (Eaglen 1984; Rosenberger 1992; Anapol and Lee 1994; Wright 2005). The more frugivorous atelines (*Ateles* spp. and *Lagothrix* spp.) tend to have broad spatulate incisors, thought to be related to peeling and ingesting fruits (Eaglen 1984; Rosenberger 1992; Anthony and Kay 1993). Alternatively, atelines that ingest a higher proportion of leaves, *Alouatta* spp. and *Brachyteles* spp., have comparatively reduced incisors that researchers hypothesize is related to a reduced mechanical loading of the anterior teeth in leaf ingestion (Zingeser 1973; Eaglen 1984; Rosenberger 1992; Anthony and Kay 1993). Kinzey (1974) remarked that the very wide incisors of *Aotus* were heavily worn with a flat wear pattern, but dietary information and feeding ecology data are still rather poor for night monkeys (Fernandez-Duque 2007).

11.5 Mechanical Properties of Fruit Ingested by Platyrrhines

11.5.1 Assessing Food Toughness

In a study of the mechanical properties of foods processed by six platyrrhine primates (*Alouatta seniculus*, *Ateles paniscus, Cebus apella*, *Cebus olivaceus*, *Chiropotes satanas* (cf. *sagulatus*), *Pithecia pithecia*) in Guyana, South America, Wright (2004) measured dietary toughness and related this to the way in which these primate species processed selected plant foods and their constituent tissues. The plant diets of these species were divided into the fourteen aforementioned tissue types (Section 11.3.2) and compared using the percentage of each tissue category in the diet (used as an estimate of processing frequency), the average toughness of processed tissues, and the maximum toughness of processed tissues (used as an estimate of peak performance). Fruit and other plant parts were often a composite of tissues that were opened with the anterior teeth and chewed with the cheek teeth. Ranks were calculated separately for plant tissues that were opened with the anterior dentition versus those tissues that were masticated with the postcanine dentition. The nonparametric Friedman and Kruskal-Wallis (Zar 1999) tests were used to compare the diets of these species. These statistics provide a ranked score of dietary demand for each primate species. The ability to incorporate multiple sympatric species in the analyses placed the dietary profile of a single species in the context of the entire community.

The most demanding masticated tissues (i.e., maximum toughness values) were processed by *Alouatta seniculus* and *Cebus apella* (Table 11.4). Although *A. seniculus* and *C. apella* were comparably ranked, their ranks were equal for different reasons. *Cebus apella* masticated (*Astrocaryum vulgare*; palm fruit, 10,909 Jm^{-2}) (Table 11.4) and breached (*Dimorphandra conjugata*; pod, 8,585 Jm^{-2}) (Table 11.5) the tissues with the greatest maximum toughness, despite the fact that the majority of its diet had relatively low toughness values. Out of 436 sampled trees in the *C. apella* habitat, 26 (6.2%) were *D. conjugata* (Wright 2005). This tree species fruited only once during the 14-month study period. This suggests that fallback resources are playing a strong role in shaping the masticatory adaptations of *C. apella*. *A. seniculus* frequently ate tough leaves, but was capable of breaching a single exceedingly tough seed coat (*Catostemma fragrans*). Out of 665 sampled trees within the *A. seniculus* habitat, one (0.23%) was *C. fragrans*. Additionally, this tree fruited

Table 11.4 Percentage of feeding bouts, average toughness (Jm^{-2}), maximum toughness (Jm^{-2}) and species with the maximum toughness values for food items that were masticated by individuals in six primate species in Guyana

Species	N[1]	% Feeding Bout	Average R	Maximum R	Species for Maximum Value
Ateles paniscus	20	51	470	1765	Bignoniaceae (unknown)
Alouatta seniculus	20	77	731	2639	Mimosoideae (Fabaceae): *Mora excelsa*
Cebus apella	22	63	669	10909	Areaceae: *Astrocaryum vulgare*
Cebus olivaceus	32	58	390	2729	Annonaceae: (unknown)
Chiropotes satanas	8	57	389	1031	Lecythidaceae: *Eschweilera sagotiana*
Pithecia pithecia	5	47	309	825	Connaraceae: *Connarus lambertii*

[1] N = number of plant tissue specimens tested.

Table 11.5 Percentage of feeding bouts, average toughness (Jm^{-2}), maximum toughness (Jm^{-2}) and species with the maximum toughness values for food items opened or breached specimens by individuals in six primate species in Guyana

Species	N[1]	% Feeding Bout	Average R	Maximum R	Species for Maximum Value
Ateles paniscus	19	49	839	2139	Polygalaceae: *Moutabea guianensis*
Alouatta seniculus	10	33	1381	7902	Bombacaceae: *Catostemma fragrans*
Cebus apella	13	37	1111	8584	Mimosoideae (Fabaceae): *Dimorphandra conjugata*
Cebus olivaceus	24	42	1042	3449	Tiliaceae: *Apeiba enchinata*
Chiropotes satanas	6	43	1385	2773	Caesalpinioideae (Fabaceae): *Eperua grandiflora*
Pithecia pithecia	5	53	1336	4329	Mimosoideae (Fabaceae): *Inga bourgoni*

[1] N = number of plant tissue specimens tested.

only once during the 14 months. Thus, both frequent use (i.e., leaves) and fallback resources (hard fruit) may play a role in shaping this species masticatory system. The sakis also placed high dietary demands on their anterior dentition. In the case of *Pithecia*, this involved breaching tough seed tissues, whereas fruit pericarps were the toughest tissues breached by *C. satanas* (cf. *sagulatus*). Those species that processed tough tissues with either the anterior dentition or cheek teeth also exhibited marked seasonal shifts in diet. These shifts include a higher percentage of leaves in the diet of *A. seniculus*, an increase in the percentage of embedded insect foraging or palm fruit exploitation in *C. apella*, and increased consumption of legume seeds in *P. pithecia*.

The importance of seasonal changes in dietary emphasis, from brittle to tough plant tissues in *C. apella* and *P. pithecia,* and tough to brittle tissues in *A. seniculus* suggests that masticatory features often identified as ‘specializations’ may actually facilitate broadening the dietary niche. These features permit the annual exploitation of a broad array of plant tissues that vary widely in toughness, and also may account for variation in the size of geographic ranges. For example, *C. apella*, *A. seniculus*, and *P. pithecia* have larger geographic ranges than *C. olivaceus*, *A. paniscus*, and *C. satanas* (cf. *sagulatus*). Although many factors play a role in the ability of a species to colonize and exploit new habitats, the ability to exploit a wide array of demanding plant and animal tissues appear to be a critical factor.

11.5.2 Food Size and Shape

Food size has a tremendous impact on masticatory function, yet it is infrequently reported in studies of primate dietary ecology. Gape changes the orientation and location of forces at the temporomandibular joint (TMJ) and the angle of contact of the tooth cusps relative to the food substrate. Thickness is arguably the primary factor influencing ingestion technique. Plant food thickness ranges from sheet-like leaves at one extreme to tree trunks at the other. Primates that exhibit relatively wide gapes are those that (1) fix their upper anterior dentition and then use the lower anterior dentition as a plane to strip away layers of bark and wood in the case of the marmosets, (2) open or scrape relatively thick/large fruits in the case of the pitheciines and atelines, or (3) open the mouth widely to place relatively large fruits or seeds on the postcanine dentition, particularly the premolars, to permit the application of relatively high muscle forces, as in the case of *Cebus* spp., particularly *C. apella*. While it is clear that marmosets exploit the thickest items when feeding (i.e., tree trunks for their exudates) and howler monkeys exploit the thinnest foods (i.e., leaves), it is less clear how the diets of "frugivores" vary according to fruit size.

We compiled average fruit thickness and breadth data to compare the dimensions of ingested fruits among *A. paniscus*, *C. apella*, *C. olivaceus*, *C. satanas* (cf. *sagulatus*), and *P. pithecia*. BW compiled data on spider monkeys and two *Cebus* species. Fruit sizes were taken from van Roosmalen (1985) for fruit species that these primates were observed to exploit in Guyana, South America. Data for the pitheciines were collected by MN at Lago Guri, Venezuela. It appears from observations of saki feeding behavior that the greatest fruit dimension is avoided or bypassed during processing. For example, fruit pods are held so that incisive forces are directed perpendicular to the food's long axis (i.e., similar to how humans eat an ear of corn). This feeding behavior eliminates any influence of pod length on jaw gape, but either pod width or breadth may influence the maximum gape used in this behavior. Thus, the results for these two dimensions are shown separately. For fruit breadth, the primate species are arrayed in ascending order according to fruit size (Fig. 11.5). *C. olivaceus* exploited the narrowest fruits followed by *A. paniscus*, *P. pithecia*, *C. apella* and *C. satanas* (cf. *sagulatus*). This, accords well with the findings for condylar length. Findings for fruit thickness (Fig. 11.6) are comparable, with only *C. apella* and *P. pithecia* trading positions.

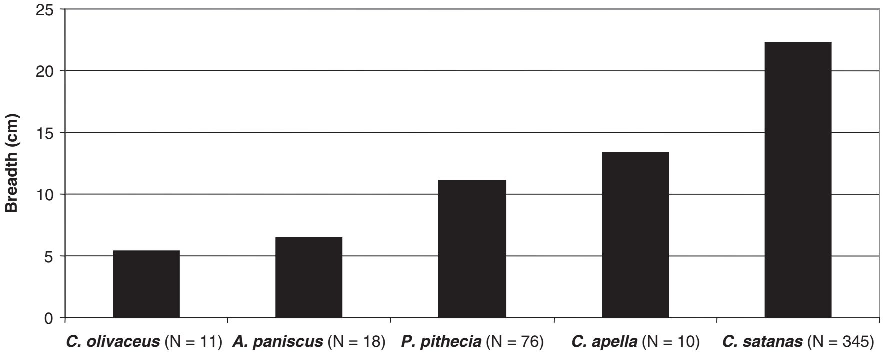

Fig. 11.5 Comparison of the breadth of fruits consumed by six Guiana Shield primates

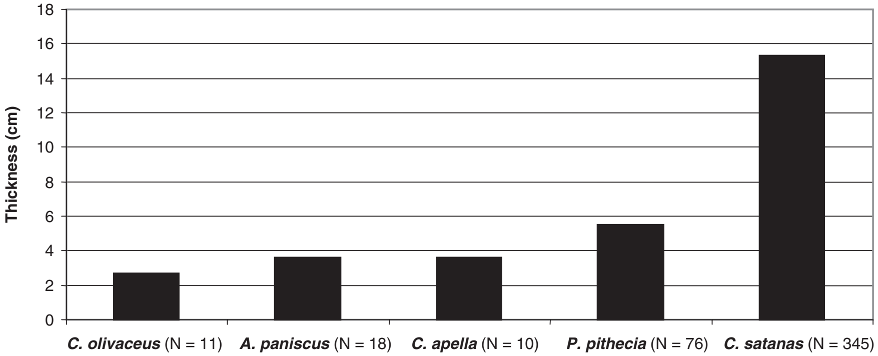

Fig. 11.6 Comparison of the thickness of fruits consumed by six Guiana Shield primates

11.6 Characteristics of the Platyrrhine Gut and Digesta Retention

Most platyrrhines have a generalized gut with some modification in the hindgut (Chivers and Hladik 1980; Lambert 1998). Enlargement of the colon and/or cecum increases the probability that fermentation will improve digestion of harder-to-digest foods, such as dietary fiber and complex sugars. There have been a number of in vivo estimates of digesta retention using indigestible markers, beginning with Milton's (1984a) study of 14 primate species. The measurement of time to first appearance (TFA) of a marker, also referred to as transit time, has been the most commonly used method of estimating digesta retention in primates to date. However, Lambert (1998), and especially Van Soest et al. (1983), noted that mean retention time (MRT) would more accurately estimate retention capability. A major problem of TFA is that the precise time of day the marker is fed to an animal affects the TFA much more than the MRT. Nevertheless, we are obliged to use TFAs here because they are currently available for more primate species than are MRTs (in addition to Milton 1984a 1998; see Power 1996; Power and Oftedal 1996 for callitrichines: Edwards and Ullrey 1999 for *Alouatta* spp.; and Norconk et al. 2002 for *Pithecia pithecia*).

Platyrrhines apparently move digesta through their gut relatively quickly, often within three to eight hours (Lambert 1998). A short TFA suggests that most platyrrhines do not digest much of the cell wall fraction, which can be considerable even in fruit (see Section 11.6.1). Instead, their strategy (at least during active periods) is to move the indigestible ballast of digesta (e.g., seeds, dietary fiber, and chitin) through the gut relatively quickly to make room for more easily digestible foods (Foley and Cork 1992; Power and Oftedal 1996). Only a few platyrrhines, such as *Alouatta* spp. and *Pithecia* spp., appear to retain digesta for longer than their daily period of activity (i.e., longer than 9 to 10 hours. Compare these data with the much longer TFAs in catarrhines documented in Lambert 1998). Interestingly, some platyrrhines adjust the intake of difficult-to-digest food items to occur before a long sleeping or resting period (Chapman and Chapman 1991; Heymann and Smith 1999). By ingesting fibrous foods late in the day, they may both improve digestion and nutrient extraction (at least some platyrrhines are known to defecate only during waking hours (Milton 1998; Norconk et al. 2002)), and shift the energy expended in food search during active periods to digestion during resting periods.

In platyrrhines, the smallest-bodied members of three of the clades have relatively longer TFAs than their larger-bodied relatives. Power and Oftedal (1996) showed experimentally that *Cebuella* and *Callithrix* slowed transit time on a diet of gum arabic compared with TFA on a baseline (non-gum) diet whereas no difference in TFA was found with three larger-bodied tamarins (*Saguinus fuscicollis*, *S. oedipus*, and *Leontopithecus rosalia*). The tamarins, unlike the marmosets, also exhibited reduced digestibility on the gum diet. *Cebuella*, who is most dependent on gum in the wild, had the longest TFA (6.3 hours: Power and Oftedal 1996) of the four callitrichines tested. Among pitheciines, *Pithecia monachus* (Milton 1984a) and *P. pithecia* (Norconk et al. 2002) have TFAs in excess of 15 hours, compared with the estimated five hours for the two larger genera, *Chiropotes* and *Cacajao* (Milton 1984a). Finally, body mass is similar among the atelines, but *Brachyteles*, the largest-bodied of the group, has a transit time of about eight hours (Milton 1984a), compared with the 25- to 32-hour average transit time for particulate markers in the smaller-bodied *Alouatta* spp. (Edwards and Ullrey 1999). The ability to use more ubiquitous resources such as leaves and gums can also influence home range size and energy invested in travel. *Cebuella*, *Pithecia*, and *Alouatta* all have relatively small home ranges and shorter daily paths than sympatric close relatives, *Saguinus*, *Chiropotes*, and *Ateles*, respectively (Milton 1988; Strier 1992; Soini 1993; Di Fiore and Campbell 2007; Norconk 2007).

Gut adaptations and/or intake of fibrous foods (especially the soluble fibers in gums) may result in increased retention of digesta and improve the competitive abilities of these platyrrhines by giving them access to more ubiquitous resources (i.e., gums in the case of the callithrichines and leaves for *Alouatta* and *Pithecia*). The mechanisms might seem counter-intuitive in that high fiber diets are generally considered useful to increase passage rate and decrease constipation in humans. Nevertheless, with the proper gut adaptations, soluble fibers are easily retained (Foley and Cork 1992); whereas insoluble fibers are generally assumed to increase passage rate (e.g., wheat bran). However, finely ground insoluble fibers do not cause laxation in humans (Wrick et al. 1983). Thus, chewing food very thoroughly may increase digesta retention in hind-gut fermenters like the Platyrrhines.

11.7 Nutritional Characteristics of Platyrrhine Diets

11.7.1 Difficulties Comparing Nutritional Characteristics of Plant Parts Ingested by Platyrrhines

The data set in Table 11.6 is a summary of the nutrient composition of at least 128 plant species, with essentially no overlap and very few unidentified species.

Table 11.6 Estimated nutritional values of food items from: Hladik et al. 1971; Gaulin and Craker 1979; Garber 1984, 1993; Nash 1986; Brown and Zunino 1990; Oftedal 1991; Castellanos and Chanin 1996; Power 1996; Silver et al. 2000; Norconk and Conklin-Brittain 2004 and unpublished data; and Hanson et al. 2006. Total non-structural carbohydrates (TNC) = *100 – %NDF – %lipids – %protein – %ash*. Estimated metabolizable energy (ME) was calculated using the general physiological fuel values of 4 kcal/g for TNC and protein, and 9 kcal/g for lipids (NRC 2003; Conklin-Brittain, Knott and Wrangham 2006)

Food (N)	% NDF	% Lipid	% CP	% Ash	% TNC**	kcals/100g
Exudates (3)	0*	0	18.7	2.9	78.4***	388.4
Arils & Palms (9)	29.7	34.8	7.5	2.5	25.5	445.2
Fungi (4)	74.9*	1.3	9.6	3.3	10.9***	93.7
Fruit Pulp (61)	25.7	4.3	7.6	4.5	58.3	299.0
Whole Fruit (33)	41.8	5.9	8.4	5.6	38.3	240.0
Flowers (18)	44.1	2.3	16.8	6.7	30.1	208.4
Seeds (35)	35.5	15.4	8.9	2.5	37.6	324.6
Young Leaves (34)	51.4	1.7	20.1	6.5	20.3	176.6
Mature Leaves(16)	58.3	1.5	14.4	8.0	17.7	141.7
Insects † (4)	32.8	16.4	45.3	2.8	2.7	339.5

† The category ‘Insects’ is a combination of adults and immatures.

* NDF= neutral-detergent fiber or total insoluble fibers. Exudates contain substantial quantities of soluble fiber, which is usually not measured by NDF. In the case of fungi, however, soluble fibers are contaminating the NDF (see Hanson et al. 2006), elevating the value considerably.

** TNC = total non-structural carbohydrates include starch, mono- and disaccharide sugars, and soluble fibers. The soluble fibers are fermented, giving 3 kcal/g fermented material, as opposed to the 4 kcal/g of digested sugar or starch. However, we are assigning 4 kcal/g of the total TNC because we have no data indicating how much is fiber and how much is starch and sugars (Conklin-Brittain, Knott and Wrangham, 2006).

*** These numbers are either mostly soluble fiber in exudates, or in the fungi, artificially low because most of the soluble fiber stayed in the NDF.

Sites from Venezuela, Belize and Panama are the most strongly represented. Not all of the datasets used, however, were as complete as the Lago Guri, Venezuela data. For example, none of the howler monkey datasets reported lipid content, not even for the fruits. Studies of leaf-eating monkeys generally assume that the lipid intake is very low, so it has never been measured, and hence there has never been a study of howler monkeys designed to test this assumption. As a consequence of this, using the small number of leaves in the Lago Guri data, and comparing that to a very large dataset from Kibale Forest, Uganda (Conklin-Brittain unpub. data), we have assigned approximate lipid values, one for leaves, one for flowers, and one for fruit. We chose values that may be lower than reality because fat content so heavily influences energy content (i.e., 9 kcal/g for fat versus 4 kcal/g carbohydrates and protein), and we did not want to artificially elevate the ME values. We wanted to keep this data set purely Neotropical, and therefore we used the African data only to reassure ourselves that we had chosen reasonable values.

In addition, different laboratory methods have been available historically (i.e., during the time span of these reports), making it difficult to combine all of these data, especially with respect to fiber analysis. Thus, the most historical data set (Hladik et al. 1971) has had a conversion factor applied to “update” the fiber values

(National Research Council (NRC) 2003: Table 3.2, pp. 65–66). On the one hand, this is worthwhile because this study adds species not repeated in other reports. On the other hand, conversion factors generally blur the detailed complexity that may exist.

A different conversion factor was applied to fiber values reported by Castellanos and Chanin (1996). They published the largest and most complete nutrient analysis of spider monkey diets to date, but the fiber values are lower than we expected. We strongly suspect that they reported acid-detergent values rather than neutral-detergent values, but there is insufficient detail in the methods to determine if this is indeed the case. Consequently we applied the conversion factor recommended to convert ADF values to NDF values, in NRC (2003: Table 3.2, pp. 65–66) because acid-detergent values cannot be used in the calculations of energy content (Conklin-Brittain et al. 2006).

11.7.2 Nutritional Characteristics of Plant Parts Ingested by Platyrrhines

The report that exudates have zero fiber is not accurate (Table 11.6); this is a reflection of the method used to quantify fiber. Neutral detergent only extracts insoluble fiber, and exudates like gums are mostly or completely soluble fibers (complex non-starch polysaccharides or NSP). The procedure for assessing Total Dietary Fiber (TDF) measures insoluble and soluble fractions separately, but it is very expensive and rarely used except on human foods. In the system we are reporting here, the percentage of NDF, protein, lipid and ash are subtracted from 100% to calculate percentage of total nonstructural carbohydrates (TNC) and the soluble fibers (NSP) are therefore included in the TNC by default. This means that the physiological fuel value of 4 kcal/g of carbohydrate is probably too high, but we do not know how much of the TNC is starch and simple sugars versus NSP (i.e., soluble fiber) for these wild plant exudates. The NSP are digested through fermentation (Nash 1986; Lambert 1998) in the large intestine (or cecum) and thus the physiological fuel value is at most 3 kcal/g of NSP (Conklin-Brittain et al. 2006). Thus the ME value is probably a slight overestimate for the callitrichine genera.

Ingestion of arils by platyrrhines is underestimated in our summary of feeding behavior (Table 11.1) because primate ecologists tend to lump arils with fruit or seeds. However, arils are widely known for their lipid-rich qualities (e.g., *Virola* spp. and palm fruit) (Aguiar et al. 1980; Howe and Vande Kerckhove 1981; Moermond and Denslow 1985; Forget 1991). Fruit-producing arils are often characterized as bird-dispersed fruits (e.g., Janson 1983), but they also figure prominently in *Ateles* (Russo 2005; Russo et al. 2005), *Pithecia pithecia* (Norconk and Conklin-Brittain 2004) and *Callicebus torquatus* diets (Palacios et al. 1997).

The fungi values used in Table 11.6 are exceptionally high in NDF. According to Hanson et al. (2006) the analyses used were not the traditional NDF procedure because there were severe filtering difficulties. A method equivalent to the TDF method was used and as a result all fibers, soluble and insoluble, are contained within, and therefore elevate, the value listed here as "NDF". The NDF usually does not include soluble fibers. Fungi were equivalent to fruit pulp in terms of crude protein. This suggests that fungi could be a seasonal protein substitute for ripe fruit for *Callimico* (Porter 2007), but ME values of fungus were by far the lowest in our sample. Hanson et al. (2006) conclude that digestion trials are needed to better understand the nutritional value of fungi.

Since NDF acts as a feeding deterrent (Wrangham et al. 1998), adding ballast but not nutritional value for nonspecialists, it is not surprising that fruit pulp is the most widely used platyrrhine food type (Table 11.1). Fruit pulp is among the least fibrous of foods and has the second highest (and most accessible) total digestible carbohydrate component (Table 11.6). Whole fruit, where both pulp and seeds are chewed up and digested, can have considerably more fiber than the fruit pulp in this data set (Wrangham et al. 1993).

Flowers are moderately high in fiber too, and their protein content is as high as leaves. Nectar can be an important dry season resource (Garber 1988, 1993; Terborgh 1983), but the nectar in flowers would have to be sampled separately if it is important to differentiate it from the rest of the flower. The TNC fraction, where you would expect to find the nectar sugars, is lower here than that for fruit pulp and even whole fruit. The ME of nectar from resources like *Symphonia globulifera* would perhaps resemble exudates more closely than the flowers in this sample.

Seeds are more energy dense than are fruit, flowers or leaves. It is not surprising that most of the larger ($>$1 kg body weight) primates eat seeds. Seeds ranked relatively high in ME due to their high lipid levels, but are challenging resources since they are often protected mechanically (see above; Kiltie 1982; Lucas et al. 2000) or chemically (e.g., Waterman and Kool 1994; Guimarães et al. 2003). They are also relatively low in protein.

Young leaves in this summary are somewhat, but not dramatically, different from mature leaves. This sample represents mature leaves that are actually eaten, so it is not surprising that they would be nutritionally similar to young leaves. Overall both leaf types are not very energetically dense.

Our small insect sample includes adults and immature stages combined. Soft-bodied insects, such as caterpillars, are likely to have a much higher ME value (Milton 1984b) and are important seasonal resources for some platyrrhines (Veiga and Ferrari 2006). Insects, as with exudates and fungi, need more nutrient analyses performed on a greater diversity of species.

11.7.3 Estimating Metabolizable Energy (ME) Intake in Platyrrhines

We have intensely scrutinized the data from the literature and summarized it according to food type in Table 11.6 and consumer species in Table 11.7. To create Table 11.7, the percentage of time spent feeding on a given food type (Table 11.1) was multiplied by the amount of each nutrient in each food type (Table 11.6), giving

Table 11.7 Nutrient and energy densities of the diets consumed by 16 platyrrhine genera and rank of platyrrhine genera based on the estimated energy density of their diets. These weighted averages were calculated by multiplying the percentage of each food type in the diet (Table 11.1) times the nutrient values for each food type (Table 11.6). Body mass estimates are averaged from Smith and Jungers (1997: Table 1)

Primate genus	Body mass (kg)	NDF[1] g/100 g of diet	Lipid g/100 g of diet	CP[2] g/100 g of diet	Ash g/100 g of diet	TNC[3] g/100 g of diet	Estimated ME[4] kcal/100 g of diet	Rank
Cebuella	0.12	11.9	5.3	25.4	2.9	54.5	367	1
Callithrix	0.37	16.9	7.1	27.3	3.1	45.6	355	2
Saguinus	0.48	25.3	8.9	25.5	3.3	36.9	330	3
Callimico	0.48	42.6	8.4	23.8	3.4	21.8	258	13
Leontopithecus	0.59	24.9	6.6	18.2	3.8	46.5	318	5
Saimiri	0.81	33.4	11.2	31.9	3.8	19.6	307	8
Aotus	0.93	38.8	3.0	14.0	5.7	38.6	237	14
Callicebus	1.05	30.9	7.6	10.6	4.1	46.9	298	10
Pithecia	2.23	35.4	12.1	10.4	3.5	38.7	305	9
Chiropotes	2.86	30.6	10.4	9.7	3.4	45.9	316	6
Cebus	2.96	29.8	8.8	20.8	3.8	36.7	310	7
Cacajao	3.05	31.1	11.2	8.3	2.9	46.5	320	4
Alouatta	6.32	41.6	2.5	14.0	5.9	35.9	223	16
Lagothrix	7.68	27.9	5.1	11.6	4.3	51.1	296	11
Ateles	8.56	29.1	4.0	9.2	4.8	52.9	284	12
Brachyteles	8.84	40.4	3.0	14.1	5.6	36.9	231	15

[1] NDF = neutral detergent fiber

[2] CP = crude protein

[3] TNC = total nonstructural carbohydrates

[4] ME = metabolizable energy.

the estimated grams of each nutrient in the diet for each primate genus (Table 11.7). Using these values, the metabolizable energy as kcal per 100 g of diet was calculated using the physiological fuel values 4 kcal/g carbohydrate and protein and 9 kcal/g lipid as discussed above.

Classic energetics studies state that the smaller the mammal the higher the energy requirements per kg of body mass (Blaxter 1989, pp. 123–133). In addition, and because of gut size restrictions in small animals, they need a higher caloric density in their food compared to larger mammals (Robbins 1993). Our values listed in Tables 11.1, 11.6, and 11.7 are the result of averaging values from various study sites and plant foods from all around South and Central America. Nevertheless, our data sets comply with these over-arching principles regarding body mass and caloric density of food (regressing kcal/100 gm of diet against body mass, Table 11.7; $r^2 = 0.27$, $p = 0.041$). Consequently we feel confident that our summaries in Tables 11.6 and 11.7 are reasonable.

The ability to eat higher fiber diets is supposed to increase with increasing body size; however, we did not find that to be true using this data set ($r^2 = 0.11$, $p = 0.20$). On the other hand, removing *Callimico* because they eat so much fungus and the fiber analysis of fungus was problematic, and removing *Aotus* because their intake of insects (a somewhat low fiber food) was perhaps underestimated, the rest of the genera follow the rule that fiber concentration increases with body size ($r^2 = 0.31$; $p = 0.04$).

Using our nutritional sample as representative of Neotropical plants, we found that *Cebuella* and *Callithrix*, the smallest-bodied platyrrhines, had the highest ME intakes due to the very high proportion of exudates in their diets (Table 11.1). The two closely related species, *Saguinus* and *Leontopithecus*, ranked lower than the marmosets, apparently due to higher intake of fruit pulp. A better year-round estimate of nectar intake (for *Saguinus*) and estimating insect intake separately for soft-bodied and hard-bodied insects may increase the ME estimate for tamarins. Nectar intake of 22.1 and 30.6% for a dry season month for *Saguinus fuscicollis* and *S. mystax*, respectively (Garber 1988:101), suggests that ME is underestimated for these tamarins. Closely related *Callimico* shows a distinctly different pattern than the marmosets and tamarins, ranking near the bottom in ME due exclusively to their high ingestion of fungi. Unlike insects that provide a mix of total digestible carbohydrates depending on NDF and lipid values, fungi analyzed by Hanson et al. (2006) appear to be uniformly low in lipids and protein, and high in NDF. High molar shearing crests may facilitate reduction of fungus particle size and improve the potential for digestion of *Callimico*'s key fallback food in the dry season (Hanson et al. 2006; Porter 2007).

Pithecia, ranked below the two other pitheciines that ingest a higher proportion of seeds. Presently, dietary studies suggest that *Pithecia* has a more diverse diet than *Chiropotes* or *Cacajao*, which means a lower proportion of seeds. The estimate of lipid intake for *Pithecia* is the highest for the platyrrhines based on combined seed and aril intake (Table 11.1), but the sakis also have a high fiber intake which reduces their ME estimate. The sister group to the pitheciines, *Callicebus*, ranked just below *Pithecia*. Interestingly, their diets appear to be quite similar if the intake of seeds (high in *Pithecia*; low in *Callicebus*) is exchanged with the intake of fruit pulp (low in *Pithecia*; high in *Callicebus*). Both ingest more young leaves than *Cacajao* and *Chiropotes*, but due to the relatively few species that are well represented in dietary studies it is difficult to capture the diversity in *Callicebus* spp.

The atelines all rank in the lower third in terms of ME estimates. The general prescription for a diet high in ME is one that is high in lipids and low in NDF. Fruit pulp, the major component of *Ateles* diets, is relatively low in both NDF and lipids. *Ateles* and *Lagothrix* both have relatively high intakes of fruit pulp, but ingestion of insects by *Lagothrix* appears to be the factor pushing them just above *Ateles* in ME rank. *Brachyteles* and *Alouatta* rank last among the platyrrhines due to their high intake of young leaves and perhaps a fallback strategy of ingesting some mature leaves (although the differences between the two in our composite database were not great). There are three possible problems with the ateline data. First, the ME estimate for *Ateles* would be more accurate with an improved estimate of the contribution of arils to their diets. Second, a recent study of *Brachyteles* (Talebi et al. 2005) suggests that fruit intake is higher than was reported in earlier studies (Milton 1984c; Strier 1991). The ME we obtained for *Brachyteles* is based on a diet that is about half leaves and half fruit, (i.e., close to that of *Lagothrix*). Third, the relatively low apparent protein value for *Ateles* is a reflection of the balance of intake that is weighted heavily toward ripe fruit. While reports of *Ateles* spp. diets are somewhat variable (leaves ranging 7–17%: Di Fiore and Campbell 2007; Table 10.3) our choice of a representative intake of 11% (Table 11.1) is not low for many studies. Thus, our finding could indicate a protein value that is lower than expected, but accurate for the animal, or it could be related to a broader life history strategy, which for *Ateles* spp. is among the slowest of the non-hominoid primates (Strier 2006; Di Fiore and Campbell 2007).

Saimiri and *Cebus* are closely ranked in the middle of the ME values just below the callithrichines and larger-bodied saki-uacaris (Table 11.7). The insect component of their diets was the highest of any non-callitrhichine and the dietary figures we used for *Saimiri* suggest that they have the highest intake of insects among platyrrhines. We suspect that their rank in terms of ME may be higher with a better estimate of the insect component of their diet. The dietary composition we used for *Aotus* had a relatively high intake of young leaves, four times that of *Saimiri*, but probably a lower estimate of insects than is realistic (Fernandez-Duque 2007). As a result, the position of *Aotus* in the ranking near the bottom may be too low.

11.8 Integrating Morphology, Dietary Properties and Nutritional Data

To explore potential relationships among masticatory morphology, dietary properties and nutrient intake in platyrrhines, we created a single summary variable from each dataset that attempts to capture the overall diversity across the clade. In some cases, we calculated this descriptive index for all available species. However to facilitate comparing the three datasets, we averaged species data at the generic level. All 16 extant platyrrhine genera are represented in the morphological and nutritional datasets, while only six genera have available data on dietary mechanical properties.

We combined several measures of masticatory apparatus form to build a biomechanical robusticity index for platyrrhines. Similar to Anapol and Lee (1994), we averaged z-scores for 10 relative measures of the masticatory apparatus related to bite force production, load resistance and dental function to generate a robusticity score for a species (Fig. 11.7). The two pitheciines, *C. satanas* and

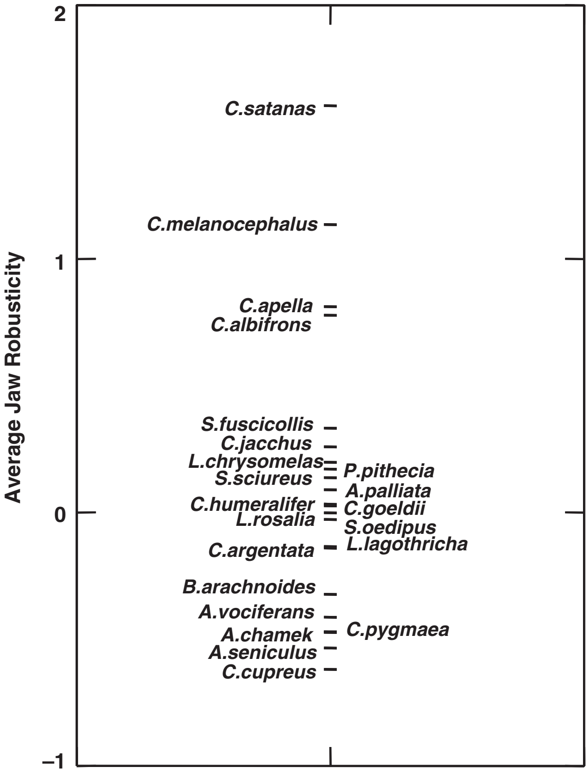

Fig. 11.7 Plot of average masticatory apparatus robusticity for 22 platyrrhine species. To estimate average jaw robusticity, we first calculated z-scores for 10 variables related to masticatory apparatus bite force production, load resistance and dental function: (1) M_1 biting efficiency, (2) symphysis length shape, (3) symphysis width shape, (4) corpus depth shape, (5) corpus width shape, (6) condyle width shape, (7) lower incisor area shape, (8) maxillary canine volume shape, (9) lower molar area shape, and (10) shearing crest length shape. We used the absolute values of z-scores for the final two measures (#9, #10) given that extremes represent mechanical solutions to different challenges posed by primate diets (see text for discussion). Shapes were created by dividing by the moment arm for biting at the M_1 or incisors. Z-score values for these measures were averaged to obtain an estimate of average jaw robusiticty in a species. In some species, data were unavailable for all 10 measures. We included species that had 6 or more of these dimensions in their average. Data for lower incisors was taken from Rosenberger (1992) and canine volumes from Thoren et al. (2006). Sources for molar dimensions (#9 and #10) are provided in Fig. 11.4

C. melanocephalus, and the two cebids, *C. apella* and *C. albifrons*, exhibit the largest average scores for this masticatory apparatus index (Fig. 11.7). While this is not unexpected, given previous research, it is surprising that the more folivorous *Alouatta* spp. and *B. arachnoides* are not differentiated from other fruit- and insect-eating platyrrhines. These results suggest that the larger size of these animals may provide them sufficient performance abilities in chewing leaves and/or their diet may not be as tough as previously thought (Teaford et al. 2006).

We represented the dietary mechanical properties dataset using the mean of the average toughness estimates taken from masticated (Table 11.4) and breached (Table 11.5) items, respectively. While there are inter-specific differences in toughness values between masticated and breached items, their average is adopted as a broad measure of overall loading experienced in the masticatory apparatus during feeding. The dataset from Turtle Mountain was supplemented with dietary toughness data from a two-month study of common marmosets (*Callithrix jacchus*) at Estação Ecológica do Tapacurá Pernambuco, Brasil (Vinyard et al. n.d.).

The metabolizable energy estimate (ME) from Table 11.7 represents variation in dietary nutrition among platyrrhine genera. Because this dataset is negatively correlated with body mass among platyrrhines, we examined both the absolute ME and the residual ME values from regression on body mass.

11.8.1 *Comparisons of Metabolizable Energy (ME), Overall Masticatory Apparatus Shape and Average Dietary Toughness*

Metabolizable energy (ME) shows little association with the jaw robusticity index (Fig. 11.8). When comparing residual ME, relative to body mass, (data not shown) a similar pattern is evident with the main difference being that the five callitrichid genera tend to have reduced relative values with respect to the remaining platyrrhines. The three genera with the most robust jaws (*Chiropotes*, *Cacajao* and *Cebus*) tend to have intermediate absolute ME estimates. Alternatively, they have higher relative ME estimates. This increase in relative ME may suggest that evolutionary changes in these three genera might have involved increasing jaw robusticity to provide the mechanical capacity for accessing structurally challenging, but energy-rich foods in their respective environments.

Dietary toughness and jaw robusticity show little association among the six platyrrhine genera represented here (Fig. 11.9). The small sample for dietary toughness precludes any definitive statements regarding the potential relationship between jaw shapes and dietary properties. While *Alouatta* and *Callithrix* have the highest average toughness values, they arrive at the top for different reasons. *Alouatta* has the highest average toughness during mastication. *Callithrix* breaches foods, specifically tree barks, with high toughness values. Marmosets may circumvent the high toughness of barks and wood fibers by planing off layers of tissue rather than cutting through fibers. The genera with relatively robust jaws tend to exhibit

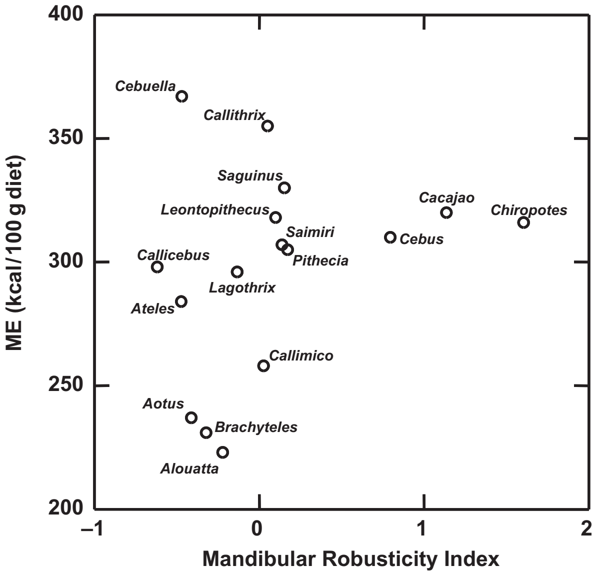

Fig. 11.8 Plot of metabolizable energy (kcal/100 g diet) versus the mandibular robusticity index for 16 platyrrhine genera

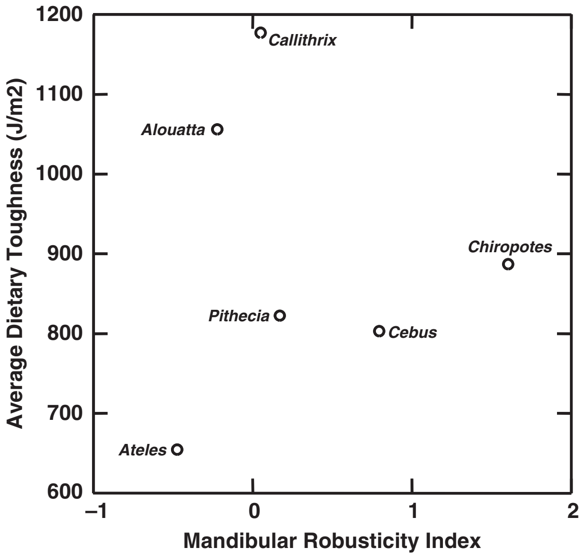

Fig. 11.9 Plot of average dietary toughness (J/m^2) versus the mandibular robusticity index for 6 platyrrhine genera

only intermediate toughness values. Collectively, this suggests that jaw robusticity may not share a particularly strong association with average dietary toughness. Jaw robusticity may be more closely associated with infrequent use of fallback or temporally limited resources. In this context, it is worth mentioning that if maximum values are compared, then *Cebus* diets are among the toughest foods sampled among these six genera (Wright 2004).

Average dietary toughness and metabolizable energy also do not show a consistent pattern across these six genera (Fig. 11.10). With the exception of *Alouatta*, there is a potential direct association between these two variables for the remaining genera. However, this pattern is contingent on the exudativorous *Callithrix* and as such really requires additional species to verify the direction of the trend. Hill and Lucas (1996) found that fiber (NDF) correlated well with toughness for Japanese macaques' (*Macaca fuscata*) leaf foods. One would expect that as fiber content (or toughness) increases, metabolizable energy would decrease. Hence it is odd to see the trend in Fig. 11.10, where as toughness increases, so does the kcals/100 g of diet (except for the *Alouatta*). Unfortunately NDF cannot be used to double check this trend (e.g., by regressing NDF against our factorially calculated ME), because the NDF value was used in part of the calculation of the ME, so they are not statistically independent values. While it remains possible that South American taxa may show similar intra-specific patterns as seen in *M. fuscata*, we need more data using an independent toughness measure to evaluate this relationship.

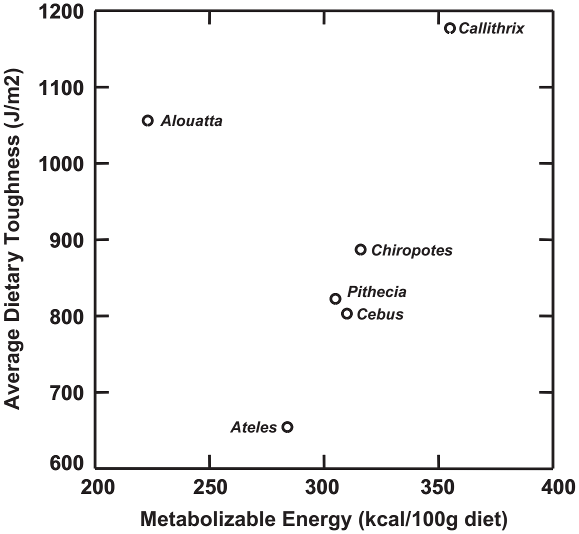

Fig. 11.10 Plot of average dietary toughness (J/m^2) versus metabolizable energy (kcal/100 g diet) for 6 platyrrhine genera

11.8.2 Synthesizing Nutrition, Jaw form and Food Properties

The extant platyrrhines represent an infraorder of at least four primate radiations, some of them dating from the early to middle Miocene (Setoguchi and Rosenberger 1987; Kay et al. 1998; Fleagle and Tejedor 2002). Compared with the more recent expansion of the cercopithecoid monkeys, platyrrhines exhibit considerable variation, in body mass and a variety of specializations, for extracting resources. As such, it is difficult to capture the diversity of the group with a few summary variables. Nevertheless, top-down analyses can be an effective means to illuminate patterns and point out deficiencies in the data. Based on our summary measures of nutritional intake and masticatory apparatus, only the larger bodied pitheciines (*Cacajao* and *Chiropotes*) had both relatively high ME intake and robust jaws. The callitrichines showed nearly the opposite pattern of having a high ME intake (by virtue of the proportion of gums in their diet) and relatively low jaw robusticity.

We are careful to point out that a poor fit between these two variables as we constructed them does not signify that nutritional and mechanical data are unrelated in platyrrhines. First, these variables could be correlated in certain species or clades. Second, other specific nutritional and mechanical variables, rather than our summary measures, may be related across platyrrhines. Finally, examining patterns at the generic level may have obscured important relationships among species. Discovering whether these potential relationships exist will require additional data and future analyses. Therefore, our results do not preclude the co-evolution of masticatory form and dietary nutrition in platyrrhines. Based on these data, however, any co-evolution linking dietary nutrition and jaw robusticity appears to follow species- or clade-specific patterns that likely differ throughout the infraorder.

We also failed to demonstrate clear relationships between dietary mechanical properties and either jaw robusticity or metabolizable energy. Our attempt to compare food properties across platyrrhines is somewhat premature because of the lack of available data. Therefore, we reserve any conclusions regarding these potential relationships. Data are needed both for additional species and other mechanical properties. Describing the mechanical variation in diets must be a priority for future studies of platyrrhine feeding adaptations. Data on food mechanics should also be coupled with detailed analyses of fruit availability and abundance in order to assess the role of fallback or temporally limited resources in shaping diet, ranging, and masticatory anatomy among platyrrhines. Fallback resources are often aseasonal resources and widely available (e.g., bark, leaves, tree exudates), but are used for only a subset of the year. Fallback foods are not considered to be preferred resources (i.e., not taken in the relative abundance in which they occur) whereas seasonally exploited resources, even if difficult to access, are taken disproportionately to their abundance. This difference is critical for differentiating the feeding strategies of primates.

Having stated these caveats, we provide a final assessment of our analysis. Platyrrhines illustrate an incredible diversity of morphology and diet in Primates. They are similar in that all are essentially arboreal and ingest fruit when it is available. Plant diversity in the Neotropics has enabled the evolution of at least four radiations – they occur in highest densities in Amazon Basin forests near the equator where plant diversities are also highest (Peres and Janson 1999). Despite the high level of diversity, we identified two patterns that help to define the platyrrhines. Within-clade (subfamily) variation tends to involve either ME or mandibular robusticity while the other variable(s) remain relatively stable (Fig. 11.8).

Cebus and *Saimiri* are very different in social behavior and in the components of their diets, but multiple species are sympatric and some (*C. apella* and *S. sciureus*) form mixed-species groups (Terborgh 1983; Podolsky 1990). From our analysis, differences between these genera lie in mandibular and dental robusticity while metabolic intake is very similar. Among pitheciines, *Pithecia* spp. have a broader geographic and habitat distribution than *Chiropotes* and *Cacajao*. By adding the fourth member of this clade (*Callicebus*) the pitheciines span the entire continuum of diversity in platyrrhine mandibular robusticity (Fig. 11.8). *Chiropotes* and *Cacajao* are largely allopatric, but both are sympatric in some parts of their range with *Pithecia,* and with both *Pithecia* and *Callicebus* in the Amazon Basin. *Pithecia* and *Callicebus* are the smaller-bodied generalists that add leaves and insects to seeds to form their primary diet. As in the cebines, the range of ME variation in the pitheciines is very low.

While allometric differences help explain variation in the cebine and pitheciine radiations, a different pattern emerges in the atelines. Variation in mandibular robusticity among atelines is low, but with a considerable range of variation in dietary ME (Fig. 11.8). Yet, the four genera present a dispersed cluster with relatively low ME and low robusticity. A similar pattern is demonstrated within callitrichines clustering in the high ME, low mandibular robusticity quadrant. In this clade, the smallest species are the most specialized – the opposite pattern of the pitheciines.

11.9 Future Directions in Studying Platyrrhine Feeding Adaptations

It is commonplace for review chapters to call for improvements in data collection and analysis. We are no different and we think that these statements serve to remind us that more precise data will further our efforts in studying platyrrhine feeding adaptations. With respect to morphometric analyses of jaw mechanics, we argue that (1) additional in vivo studies are needed to validate morphometric proxies of mechanical abilities and (2) morphometric measures can be improved to provide more precise estimates of mechanical ability (e.g., Deagling 2007).

Analyses of dietary mechanical properties in the field are still in their relative infancy. We examined data on dietary toughness in this chapter, but the technology is currently available to measure other properties such as stiffness, hardness and friction in primate diets (Lucas et al. 2001). In particular, it would be helpful to document variation among platyrrhines for two fragmentation indices, ($E^*R^{0.5}$) and $(R/E)^{0.5}$ (Agrawal et al. 1997; Lucas et al. 2002; Lucas 2004). These indices describe stress-limited and displacement-limited patterns of food breakdown, respectively, and would help to document expected morphological features that might be associated with a particular species diet. We anticipate that documenting variation in food properties will provide some of the most important advances in our understanding of platyrrhine jaw and tooth form over the next decade.

The relationship between primate feeding ecology and an interest in nutrition is gaining ground with more researchers recognizing the relevance of not only quantifying intake, but also collecting relevant food parts for nutritional analysis. Of particular importance are seasonal variation in food availability, the use of fallback resources, and the intake of nutrients and feeding deterrents. In the past, primate research has practiced the conventional wisdom that for herbivores and omnivores it is more important to balance nutrients and avoid secondary plant compounds than to determine the energy content of foods. However, increasing evidence shows that reproduction in primates, and hence fitness, is dependent on overall energy intake (Knott 2001, 2005; Emery-Thompson et al. 2007). The feeding selectivity that we see in herbivorous and omnivorous primates is still meant to achieve optimal energy intake, although initially the consumer needs to balance nutrients and avoid digestion inhibitors. The practical impact of this is that complete analyses have to be performed on all foods in order to continue making progress with this theory. To continue using factorial estimates of metabolizable energy as the nutrition variable, a complete laboratory analysis consists of protein, lipid, total ash, and neutral-detergent fiber (NDF). Total dietary fiber (TDF) might be preferred over NDF for the gummivorous species, because it quantifies the soluble fiber as well as the insoluble fiber.

Finally, we urge further integration of phylogenetic, morphological, nutritional, dietary mechanical, and ecological research methods in studying platyrrhines. Even though we saw little evidence for associations among these different data sets in platyrrhines, we still consider the integration of these otherwise disparate research agendas as a great source of potential advancement in our understanding of platyrrhine feeding adaptations. When possible, we recommend collecting all four kinds of data in single species or population. As part of this integration, traditionally lab-based techniques need to be taken to the field and joined with behavioral ecology research on free-ranging platyrrhines (Wright 2005; Williams et al. 2008). In addition, non-invasive captive animal nutritional work comparing in vivo digestibilities and dietary properties, as well as the effects on digestibility of different particle sizes resulting from different tooth morphologies may help identify where these different areas of research can work together. Through increasing our precision and integration, we hope to further our understanding of both the range and patterns of adaptations for accessing foods among platyrrhine primates.

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