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Physiological Ecology of Howlers (*Alouatta*): Energetic and Digestive Considerations and Comparison with the Colobinae

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Remarkably little attention has been focused on the physiological ecology of free-ranging primates. Yet without such information, it may prove difficult to advance our understanding of factors influencing the dietary behavior of wild primates much beyond its present state. Mantled howlers (Alouatta palliata) *have been studied in terms of some features of physiological ecology. Results of this work have helped to clarify some factors influencing howler and other primate food choices in the natural environment and have called into question various assumptions about leaf-eating primates. For example, though howlers eat considerable foliage, they do not exhibit a lower than predicted basal metabolic rate, nor do available data suggest that secondary compounds strongly influence howler food selection. Comparison of howlers with members of the Colobinae reveals some differences in features of their respective energetic and digestive physiology and raises timely issues for future research.*

KEY WORDS: primates; monkeys; physiology; digestion; energetics; plant foods; fermentation; leaves; secondary compounds; *Alouatta*; Colobinae; howlers; colobines.

INTRODUCTION

Most physiological studies of nonhuman primates are medical in nature. Comparatively little attention has been devoted to aspects of the

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physiological ecology[3] of free-ranging primates and such basic features as basal metabolism or pattern of digestive kinetics remain unknown for most species. Without such information, it is often difficult to understand key behaviors of particular species in the natural environment or to identify factors that may set limit niche breadth. Therefore, more attention should be focused on physiological questions related to diet and digestion as additional information on the dietary behavior and food choices of wild primates, in itself, seems unlikely to advance our understanding of factors underlying such behaviors much beyond its present state. A brief example may help to illustrate why a stronger focus on physiological studies would be particularly useful.

Protein/Fiber Ratio and Secondary Compounds

My interest in the physiological ecology of wild primates was stimulated by my fieldwork on the foraging behavior of mantled howlers (*Alouatta palliata*) in Panama in the early 1970's. I noticed that wild howlers took foods from a variety of different plant species each day, often avoiding what appeared to be edible leaves or fruits. Howlers also avoided eating most mature leaves in their habitat. To determine what underlay this selection, I collected leaf samples for chemical analysis and tested several hypotheses on herbivore leaf choice (Milton, 1979). At that time, secondary compounds were beginning to be discussed in the literature as important determinants of primate food choice (Glander, 1978; McKey, 1978; Oates, 1977, 1978), as were factors such as incomplete nutrients (Westoby, 1974; Glander, 1975) and cellulose and lignin (Oates, 1977; Milton, 1977). Results of my analyses, however, showed little obvious effect of secondary compounds on howler leaf selection. Though more than one factor appeared to influence howler leaf choice, overall, the single most important factor identified was the protein–fiber ratio of the leaf (Milton, 1979). Based on these results, I hypothesized that protein–fiber ratio would prove to be an important predictor of primate leaf choice on a pantropical basis (Milton, 1979; Milton *et al.,* 1980).

Thereafter, a large number of field investigations have been conducted on the feeding behavior and dietary constituents of leaf-eating primates, particularly members of the Colobinae, but also various howler species and some Malagasy prosimians. This information provides a broad data base from which to draw in terms of the food choices of folivorous primates and considerable useful information on the chemical constituents of many of their foods. However, our understanding of factors underlying observed feeding patterns has not advanced to a similar degree.

For example, Waterman and Kool (1995) reviewed factors suggested to influence the leaf choices of 8 colobine populations representing several species in a variety of habitats and concluded that "chemical studies in foliage indicate selection for high protein and/or digestibility and against high fiber." As hypothesized, other studies too have found protein–fiber ratio to be a robust predictor of primate leaf choice (Ganzhorn, 1989; Yeager, 1989; Mowry *et al.,* 1996). Similarly, though the influence of secondary compounds on patterns of primate food choice continues to be persistently advocated, data to support such assertions are often lacking.

Clearly new directions need to be taken if we want to advance understanding of the particular set of traits that enables a given primate to identify what is or is not suitable food in its habitat and the energetic and other factors that may constrain niche breadth and facilitate sympatry between particular primate species. Without more information on features of the energetics and digestive physiology of wild primates and investigation of the interplay between such features and potential food sources in the natural environment, we are forced to rely largely on speculation or comparisons with other herbivorous mammals—often highly specialized marsupials eating a narrow range of heavily defended plant parts, e.g., koalas, or large-bodied terrestrial ungulates.

Mantled howlers (*Alouatta palliata*) are one of the few primate species that have been studied in terms of some basic aspects of energetics and digestive physiology. These data, in combination with information on food choices and chemical constituents of the howler diet, have helped to clarify some factors which appear to influence howler foraging behavior. I review this information and, whenever possible, compare it with available data on Colobinae (1) to draw attention to physiological features of these two evolutionarily distinct primate lineages which appear to play an important role in their respective abilities to utilize the leaves of woody tree species as a principal item of diet and (2) to indicate potentially useful directions for future research. One type of comparative approach likely to produce meaningful results is that of Hume (1982), who provided illuminating and clear comparative information on gut morphology, diet selection, and digestive physiology for various species of marsupials.

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[3] Physiological ecologists examine physiological diversity in relation to the environments in which organisms live (Feder *et al.,* 1987). Nagy (personal communication) suggests that physiological ecology can be viewed as the study of physiological mechanisms aiding survival in the natural environment. Tracy and Turner (1982) provide several definitions and discussion of the subject matter of physiological ecology.

Howlers and Colobines

There is an extensive literature on food choices of howlers and colobines (Struhsaker, 1975; Oates, 1977; Hladik, 1977; Glander, 1975, 1978, 1982; Oates *et al.*, 1980; Milton, 1977, 1980; Estrada, 1984; Chapman, 1988; Davies *et al.*, 1988; Stanford, 1991; Dasilva, 1992, 1994; Maisels *et al.*, 1994). All howler species are hypothesized to occupy the same dietary niche (Milton, 1977, 1979). At all study sites, howlers have been described as primary consumers eating varying proportions of leaves, fruits, seeds (largely unripe), and flowers. No matter how much ripe fruit is available in a given habitat, howlers invariably eat some foliage each day. At some times of year, and often for weeks at a time, howlers at many sites survive on diets consisting in large part or entirely of the leaves of woody trees and vines (Glander, 1978; Milton, 1980; Chapman, 1988). Howlers generally consume immature leaves, but they also eat mature leaves of select species. *Alouatta* is generally regarded as the most folivorous New World primate genus (Eisenberg *et al.*, 1972; Rosenberger and Strier, 1989; but see Milton, 1984; Emmons, 1990).

Like *Alouatta*, all members of the Colobinae are primary consumers, but unlike howlers, they occupy a range of different dietary niches and sympatry between congeners is common. Though colobines eat leaves, fruits, flowers, and at some sites, quantities of seeds (often unripe), they typically focus much of their feeding time on leaves [estimated range, ~34 to ~81% of the annual diet, depending on species and locale (Chivers, 1995, p. 217; Stanford, 1991, p. 94, Dasilva, 1994, p. 656)]. Like howlers, colobines greatly prefer young leaves but also eat some mature leaves and, in some species, large quantities of mature leaves (Stanford, 1991; Dasilva, 1992; Waterman and Kool, 1995; Mowry *et al.*, 1996). Unlike howlers, which have a simple acidic stomach (Milton and McBee, 1983), colobines have a highly specialized, complex stomach with discrete alkaline and acidic sections (Bauchop and Martucci, 1968; Dobson *et al.*, 1984; Chivers, 1995).

Some authors, e.g., Cork (1994), describe howlers as much less folivorous than colobines. However, at some locales, e.g., Corrientes Province, Argentina, short-term data on feeding behavior and available dietary resources suggest that some howlers—troops of *Alouatta caraya*—may feed exclusively or almost exclusively on leaves for weeks at a time (K.M., unpublished data). Some howler populations and species may eat as much or more foliage per year than many colobine populations and species. As discussed below, the critical difference between these two taxa may lie in their differing degrees of dependence on fermentation or their relative abilities to deal with the chemical constituents of mature leaves or certain types of seeds or both efficiently. As both howlers and colobines are primary consumers with a focus on leafy foods, I will review the main problems posed by such diets.

Problems Posed by Leafy Diets

Though generally described as omnivores, most primates, particularly anthropoids, consistently take most of the diet from plants (Milton, 1980, 1981). As most primates are also arboreal, the plant parts they consume tend to be the leaves, fruits, seeds, and flowers of tropical forest woody trees and vines. Plant foods pose many problems to potential consumers in terms of their chemical composition. Most critical is the fact that they generally contain a high percentage of indigestible cell wall material in relation to available cell contents (Bauchop, 1978; Parra, 1978; Milton, 1977, 1979). Once the soluble cell contents have been extracted, in the absence of certain mitigating factors, the cell walls continue to occupy the same effective volume in the gut until they are defecated: the hotel hypothesis of Van Soest (1982). This sets an obvious constraint on the amount of food the feeder can process per unit time. In addition, unlike many fruits and seeds, the soluble carbohydrate fraction of woody tree and vine leaves typically is quite low, generally in the range of some 3–4% dry weight (Milton, 1979), and leafy material and other plant parts are often low in one or more essential nutrient (Westoby, 1974; Glander, 1975).

Apparently in response to the high fiber and low available energy content of leaves as food, one feature that has been amply documented in herbivorous mammals, including some primates, is microbial fermentation. Certain bacteria, protozoa, and fungi living in enlarged sections of the digestive tracts of many species are able to degrade plant cell wall components: celluloses, hemicelluloses. In this process, energy-rich, short-chain volatile fatty acids (VFAs) are produced that can often be absorbed by the host and may make an important contribution to its energy budget. Microbial protein, which is of high biological value, as well as certain essential vitamins may also be available to some hosts, depending on the site of fermentation (Parra, 1978; Van Soest, 1982; Stevens, 1988).

But efficient fermentation of plant cell wall material tends to be a time-consuming process (Van Soest, 1982; Demment and Laca, 1991). This can pose particularly acute problems for primates because most are highly mobile, arboreal animals and, as such, are not particularly large. Large body size confers decided advantages in terms of lowering energetic and other nutritional requirements per unit mass (Kleiber, 1961; Parra, 1978). Gut volume tends to scale at a constant proportion of body mass (Parra, 1978); smaller mammals may therefore have higher energetic and nutritional demands per unit volume of the gut than larger ones (Parra, 1978; Demment and Van Soest, 1985). Snipes (1994) showed that smaller mammals have proportionately more surface area—absorptive surface—in the gut than larger mammals do, perhaps to compensate for the more rapid passage rate of digesta (Demment, personal communication). But a slight advantage in surface area does not appear sufficient to overcome all of the nutritional problems posed to small mammals by leafy diets.

Body size constraints thus force most primates, regardless of their digestive strategy, to feed selectively (Parra, 1978; Van Soest, 1982; Demment and Van Soest, 1985). Finding an efficient solution to the high percentage of indigestible material present in most plant parts—fruits as well as leaves—appears to be the single greatest dietary problem in terms of food composition that anthropoids have had to resolve in their evolutionary history.

Working with various forages, Smith *et al.* (1970) demonstrated that rates of cell wall digestion are positively correlated with cell soluble content. The cell solubles did not directly contribute to the faster rate of cell wall digestion; instead, this correlation appeared to result from physical properties of the associated cell walls (Smith *et al.*, 1970; see also Sullivan, 1966). If tropical tree leaves conform to this trend, the protein–fiber ratio would appear to be a useful index for judging the potential overall energetic and nutrient returns of a leaf to the primate feeder as well as the time commitment involved in its digestion, which is an important factor for smaller-bodied herbivores such as monkeys. Accordingly, the plant-based dietary focus of anthropoids poses a diverse set of problems, and as a class, leaf-eaters may face particular challenges in terms of meeting energetic requirements. Study of selected features of primate physiology provides insight into how some problems may be resolved.

ENERGETIC PHYSIOLOGY OF LEAF EATERS

Basal Metabolism

McNab (1978) predicted that leaf-eating arboreal endotherms would show lower basal metabolic rates (BMR) for body mass than values predicted by Kleiber (1961). A lower basal rate would lower energetic costs, which could be particularly valuable to leaf eaters. The BMR of two mantled howlers (*Alouatta palliata*) in Panama were not lower than predicted. Instead, their values were about 5% above expected values (Milton *et al.*, 1979).

McNab (1986) later expanded his prediction of lower than expected BMR to include not only leaf-eaters but also eutherians feeding on fruits or invertebrates (McNab, 1986). However, data for the BMR of anthropoids indicate that most species fall approximately where predicted in terms of BMR, regardless of dietary focus (Bruhn, 1934; Scholander *et al.*, 1950; Milton *et al.*, 1979; Muller *et al.*, 1983).

If a consistent exception to this trend were to be found among anthropoids, it might be the Colobinae because of their unusual digestive system among Primates, which includes pregastric fermentation. Grazers (forb eaters)—a class which includes pregastric fermenters such as ungulates—are hypothesized to show a higher than predicted BMR (McNab, 1986). This characteristic is attributed in large part to common features of forb-based diets rather than phylogenetic affinities of the forb-eaters, which differ, e.g., ruminants versus microtines: cows versus horses.

Muller *et al.* (1983) found the BMR of two *Colobus guereza* to be slightly lower (85%) than expected values. They remarked that the question of whether this slightly low metabolic rate related more to characteristics of the natural diet of this species—primarily woody tree leaves (Oates, 1977; Cork, 1994)—or to features of its phylogenetically shared digestive system remains open. As howlers eat leaves and do not appear to have a lower than predicted BMR, it may be the phylogenetically shared digestive system of the colobines and not leafy diets per se that relate more directly to a lower than expected BMR in colobines. The structure and physiology of the colobine digestive system may relate to unusual nutritional/energetic stresses associated with some feature of their diet. Sakaguchi *et al.* (1991) found that silvered langurs voluntarily consumed a much lower dry matter intake of a commercially prepared high-fiber diet as measured in $g/kg^{0.75}$ than was the case for two macaque species offered the same diet.

The BMR of both howlers and colobines needs to be more thoroughly examined as available information is scant, sample sizes are small and questions have been raised on some features of trial protocols in both cases (McNab, personal communications; Cork, 1994). Furthermore, one cannot (a) assume that BMR in any particular case will follow the predicted value or (b) predict from BMR what active metabolism actually will be, nor (c) can one necessarily extrapolate from estimates of free-ranging metabolic rate what the BMR of a given animal actually is (Hume, 1982; Koteja, 1991).

Free-Ranging Metabolism

The energy requirements—free-ranging metabolism (FRM)—and feeding rates of animals in the field can be measured through the doubly labeled water method (Lifson and McClintock, 1966; Nagy, 1987). This costly and labor-intensive procedure may no longer be necessary in some cases, particularly in broad surveys, since Nagy (1987, 1994) has presented allometric equations to predict FRM and feeding rates for a wide range of vertebrates.

Adult howlers weigh between 6 and 9 kg. A study of the active metabolism of free-ranging mantled howlers (*Alouatta palliata*) in Panama, using water labeled with tritium and oxygen-18, showed a field metabolic rate averaging 355 kJ kg^{-1} day^{-1} (~2 × BMR) (Nagy and Milton, 1979a). We estimated feeding rate at ~54 g dry matter kg^{-1} day^{-1}, or around 1000 g wet matter day^{-1}, for an adult howler [~15% of adult body mass (Nagy and Milton, 1979a)].

The active metabolism of colobines has not been measured in the field. Using equation 22 of Nagy (1987), the FRM for a hypothetical 10-kg eutherian mammal having a generalist's diet is estimated at 598 kJ kg^{-1} day^{-1}, while its predicted feeding rate is estimated at 456 g of dry matter per day (or ~46 g dry matter kg^{-1} day^{-1}) (K. Nagy, personal communication). However, the FRM of a hypothetical 10 kg herbivorous eutherian mammal is estimated at 481 kJ kg^{-1} day^{-1} and its feeding rate at 467 g of dry matter per day (or ~47 g dry matter kg^{-1} day^{-1}) (K. Nagy, personal communication; Nagy, 1987).

Behavioral Adaptations

As the low available energy content of leaves is hypothesized to pose problems for leaf-eating monkeys, one would predict that they would show behaviors associated with energy conservation. For example, howlers appear to mitigate many potential energy problems through behavioral rather than physiological adaptations (Milton, 1977, 1978a). Such behaviors include high selectivity in feeding, a pattern of goal-directed travel from primary food source to primary food source, long periods of inactivity, the avoidance of sudden movements or rapid travel that could raise body temperature, and body postures that appear to aid in conserving or dissipating body heat. Similar behaviors have likewise been noted in other leaf eating primates (Oates, 1977; Milton, 1984; Stanford, 1991; Dasilva, 1992, 1993). Dasilva (1992, 1993) related postures and activity patterns of *Colobus polykomos* to diet and suggested that they too may rely on behavioral rather than physiological adaptations to cope with periods of low energy intake.

DIGESTIVE MORPHOLOGY AND PHYSIOLOGY

Howlers

Gut Morphology

Howlers have a fairly standard anthropoid gut in terms of sections and proportions. The simple stomach, which is not particularly large, has an acidic pH of <4.5 (Milton and McBee, 1983; Chivers and Hladik, 1980). The total length of the howler intestine is remarkably short for a fruit- and leaf-eating monkey (Hill, 1972). The howler cecum has a larger relative surface area [= actual surface area)/(length of body + head)^2 × 1000] (Hladik, 1967) than many other primate species, but similar cecal proportions are found in spider monkeys (*Ateles paniscus*), which are extreme ripe fruit specialists, and gum-feeding galagos (*Euoticus elegantulus*) (Hladik, 1967; Charles-Dominique, 1977). The colon of howlers is smooth-walled and unsacculated (Hill, 1972) and has a relative surface area almost identical to that of the small talapoin monkey (*Cercopithecus talapoin*). The relative surface area of the howler colon is unexceptional in comparison with those of various other anthropoid species that are not leaf-eaters (Hladik, 1967; Milton, 1980). Thus gut parameters do not necessarily indicate the diet or digestive strategy of the feeder.

Digestive Kinetics and VFA Production

I studied food passage rates in Panamanian mantled howlers to determine whether howlers were utilizing a power or an efficiency approach to some of the dietary problems posed by leafy foods (Bell, 1971; Janis, 1976; Milton, 1981). In the power strategy, the feeder processes a large volume of food per unit time. Because of the sheer volume of ingesta passed through the tract each day, the feeder is able to obtain sufficient energy and other nutrients, e.g., protein, to meet nutritional requirements. A power approach can have different parameters. For example, a horse can eat fairly low-quality forage but, given its body size, gut structure, and food passage rate, apparently is able to extract the energy and other nutrients it requires from the sheer volume of food processed per unit time (Janis, 1976; Bjornhag, 1994).

Contrarily, a power strategist such as a spider monkey (*Ateles* spp.) eats quantities of energy-rich, sugary fruits, which many would view as having high quality. Fruits, though high in digestible energy, are generally low in protein and, frequently, high in indigestible bulk: woody seeds and seed coats as well as fibrous pulp. Spider monkeys (*Ateles geoffroyi*) turn over ingesta rapidly [mean time of first appearance (TFA) = 4.4 hr (Milton, 1981)], a digestive strategy which should enable them to process a sufficient quantity of fruits each day to meet or almost meet protein requirements; spider monkeys supplement this basic high-fruit diet with select, protein-rich young leaves.

In contrast to the power approach, in the efficiency approach, the feeder must select foods carefully, as much of each meal tends to be held in the gut for a long period (Bell, 1971; Janis, 1976; Milton, 1981). An efficiency approach, like a power approach, can have different parameters. For example, cattle utilize an efficiency approach. Because their principal fermentation chambers are in the foregut, they can derive a high percentage of both required energy and protein and certain vitamins from foregut microbes or their by-products or both (Van Soest, 1982; Dobson *et al.*, 1984). This same condition would appear to be true of colobines. In contrast, howlers have fermentation chambers beyond the small intestine in the cecum and proximal colon (Milton and McBee, 1983) and must therefore select foods of sufficiently high quality to meet their own protein requirements as amino acids probably are not absorbed from the mammalian large intestine (Stevens, 1988), and howlers do not appear to be coprophagous.

To examine food passage rates in howlers, I mixed small plastic particles from forestry surveying tape with wild foods and fed them to caged howlers. On average, markers fed between 0800 and 0930 first began appearing in feces ~23 hr later, while markers fed at 1630 first appeared ~16 hr later. Howlers do not defecate at night. Mean time of first appearance (TFA) of markers for all trials is 20.4 ± 3.5 hr (Milton, 1981). Some markers were eliminated in feces >72 hr after the initial feeding, and I observed slight mixing of markers that had been fed on different days (Milton, 1981). This raises the possibility of (selective) retention of some food particles in the howler gut.

The study was expanded to include 9 digestion trials with 5 temporarily caged wild howlers (*Alouatta palliata*) in Panama (Milton and Demment, unpublished data). Weights of the 5 subjects ranged from 3600 to 6170 g. We fed liquid [cobalt EDTA (CoEDTA)] and particulate [chromium (Cr) mordanted onto bran fiber] markers to subjects in foods between 0800 and 0930 to estimate passage rates (per the protocol of Milton and Demment, 1988).

MTT [mean transit time: an estimate of the average amount of time a particle of marker is retained in the digestive tract (Ehle *et al.*, 1982; Wrick *et al.*, 1983)] for the particulate markers ranged between 19.0 and 27.5 hr. Median MTT for all 9 trials is 23.5 hr (Milton and Demment, in preparation), which is in close agreement with TFA results obtained in the initial trials.

Mean retention time in ruminants shows a strong relationship to body weight (Gordon and Illius, 1994). Comparative data are scant for TFA or MTT in primates. Some data (Milton, 1981, 1984; Milton and Demment, 1988) suggest that howlers have a slow passage rate in comparison with some other New World primate species and some apes. On the other hand, Clemens' (1980) data on food passage rates in vervets (*Cercopithecus aethiops*), a species smaller than howlers, show that fecal appearance of ~50% of the marker was approximately 30 hr. Similar to results for howlers (Milton, 1981), Clemens' (1980) data suggest that some fluid and particulate markers may be retained in the gastrointestinal tract of vervets for as long as 5 days.

Long retention time in howlers presumably relates to efficient digestion of cell wall material or absorption of VFAs or both in the cecum and proximal colon, activities which should help meet energetic demands (Milton, 1981; Milton and McBee, 1983). Milton and McBee (1983) hypothesized that howlers may meet ≥31% of their estimated daily energy requirements from VFAs produced in cecum–colon fermentation. Likewise, long retention time in vervets may relate to some manner to improved digestion returns, including absorption of VFAs produced at highest concentrations in the cecum and colon (Clemens, 1980; Stevens, 1988). Clemens (1980) recorded a measurable quantity of VFAs in the stomach and small intestine of the vervet, and measurable VFA production has been noted in the stomach of other mammals including the rat, rabbit, pig, horse, and dog (Stevens, 1988).

Considerably more work needs to be carried out on fermentation processes in different sections of howler and colobine guts on the actual substrates being fermented in each section and on the absorption rates of VFAs in different sections of the gut (Cork and Hume, 1983). For example, koalas, which are regarded as arboreal folivores, do not appear to digest large amounts of plant cell wall material but, instead, selectively retain and ferment solutes and fine particles in the hindgut (Cork *et al.*, 1983).

Efficiency of Howler Digestion

Digestion trials with *Alouatta palliata* in Panama eating wild foods (Milton *et al.*, 1980) show that adult howlers have an average digestive efficiency of 23% with respect to cell wall material (neutral detergent fiber; NDF) on a primarily fruit-based diet and 41% on a primarily young leaf-based diet. Sixty-seven percent of the cellulose and 63% of the hemicellulose in the leaf diet and 29% of the cellulose and 18% of the hemicellulose in the fruit diet disappeared in transit through the howler digestive tract (Milton *et al.,* 1980). We attribute lower digestive efficiencies on the fruit diet to quantities of indigestible fig seeds in the sample fruits.

Howlers have fermentation efficiencies that compare favorably with those of various other nonruminant mammalian herbivores and some ruminants (Van Soest, 1982, pp. 208, 338). All howler subjects were more efficient at degrading cellulose than hemicellulose (Milton *et al.,* 1980), the reverse of the trend generally found in nonruminant herbivores (Van Soest, 1982). Van Soest (1982) noted that hemicellulose is the most complex plant polysaccharide and the most difficult to comprehend analytically. Hemicellulose is more closely associated with lignin than any other polysaccharide fraction. In ruminants, digestibility of hemicellulose is negatively related to lignification (Van Soest, 1982; Sullivan, 1966). The wild plant foods consumed by howlers may have a hemicellulose–lignin relationship that lowers hemicellulose digestibility or produces confounding results in laboratory analyses (Sullivan, 1966).

In digestion trials with howlers, fecal nitrogen content was high and apparent digestibility of protein was low. True digestibility estimates, however, indicated that, on average, 77% of dietary protein was removed in transit from the fruit diet and 89% from the leaf diet (Milton *et al.,* 1980). Lower protein digestibility in the fruit diet appears to be related to the fact that much N in fruits presumably is bound up in fig seeds, which were digested in laboratory analyses but not in passage through the howler gut. The considerable difference between apparent and true digestibility of protein suggests that the majority of fecal N in howlers is endogenous.

On the leaf diet, all subjects remained in positive nitrogen balance (Milton *et al.,* 1980). However, on the fruit diet, both adults were in negative nitrogen balance. We estimated that wild howlers must take in 3.3 g of protein per kg^{-1} day^{-1} to remain in positive N balance, and when eating a typical leaf and fruit diet, consumed leaves must show a crude protein content of >11% for them to meet this requirement (Milton, 1979; Milton *et al.,* 1980). Most mature leaf samples from the Barro Colorado forest have an estimated protein content <11%. The mature leaves selected as foods by howlers on Barro Colorado Island are unusual in that they generally resemble immature leaves in terms of their protein/fiber ratio (Milton, 1979, 1980). For this reason they can be regarded as young leaf analogues (Milton, 1980).

Colobines

Gut Morphology

All colobines are characterized by a specialized, compartmentalized stomach. The first section consists of an alkaline (pH 5.0–6.7) compartment, the *saccus gastricus*, in which microbial fermentation takes place (Bauchop and Martucci, 1968; Chivers, 1995). A *tubus gastricus* connects the *saccus gastricus* with the pyloric region, the acidic or true stomach, which empties into the small intestine. Colobines also possess a fairly capacious cecum and proximal colon (Chivers, 1995; Kay and Davies, 1995).

Digestive Kinetics and VFA Production

Few data are available on the digestive kinetics of colobines. Food passage rates for the silvered langur (*Trachypithecus cristatus*) were studied by Sakaguchi *et al.* (1991) using Cr-mordanted ryegrass cell wall constituents as a particulate marker and Co-EDTA as a liquid marker. In subjects on a high-fiber (= 37.5% NDF) diet, liquid and solid markers passed at approximately the same rate. First appearance of particulate markers was 13.6 ± 5.4 hr, while mean transit time was 46.8 ± 6.0 hr. Estimates derived from lignin concentrations in different sections of the gut of *Colobus guereza* suggest that in this species, on average, digesta may spend 14 hr in the *saccus gastricus*, 8 hr in the cecum–colon region, and 38 hr in the total tract, excluding the small intestine (Kay and Davies, 1995).

Working with individuals of two captive colobine species—*Presbytis entellus* and *T. cristatus*—Bauchop and Martucci (1968) demonstrated a constant high production of VFAs in the *saccus gastricus* and produced data suggesting that these were absorbed. Bauchop and Martucci (1968) estimated that a 4.5-kg langur, apparently *T. cristatus*, obtained ~283 kcal per day from VFAs produced via foregut fermentation, which they judged to be sufficient to meet its maintenance energy needs (218 kcal). Colobines also have fermentation in the cecum and proximal colon (Kay *et al*, 1976), an activity which could raise energetic returns from VFA production (Kay and Davies, 1995).

The langur subjects of Bauchop and Martucci (1968) had esophageal grooves (*canalis gastricus*), a characteristic of ruminants. The esophageal groove of immature ruminants closes during suckling, permitting milk to bypass the fermentation chambers (Van Soest, 1982). This structure gradually becomes afunctional, but apparently not dysfunctional, as the young

Hladik (1978) and Ganzhorn (1989) suggested that niche differentiation in primates may relate to specific abilities to deal with particular types of secondary compounds. For example, detoxification of some secondary compounds by gut flora might permit colobines to eat foods that are avoided by sympatric simple-stomached primate species (Hladik, 1978). The ability to deal with a particular type of secondary compound might help to explain niche differentiation for species such as the golden bamboo lemur, which is highly specialized dietarily (Glander *et al.*, 1989). But secondary compounds seem unlikely as a general explanation for niche differentiation in sympatric primates beyond the broad level postulated above (Hladik, 1978).

Within and between habitats, it is obvious that many primate species converge markedly on plant foods from particular plant families and genera. For example, foods from the Moraceae tend to be eaten in quantity by numerous primates species within and between habitats on a pantropical basis (Milton, 1991). Plant parts in this family could lack toxic (or digestibility-reducing) secondary compounds; but it could also be that plant parts from this family are unusually nutritious or digestible or both and perhaps more available in space and time than those of many other plant families (Milton, 1991). In general, data on primates suggest that characteristics such as body size, features of the dentition and digestive tract, and other morphological and physiological traits, as well as patterns of habitat use, may pertain more directly to niche differentiation than the ability to detoxify particular secondary compounds, but this question remains an open one (Ganzhorn, 1989; McArthur *et al.*, 1991, Cork and Foley, 1991; Freeland, 1991).

Digestion-Inhibiting Compounds

Tannins are the most frequently discussed class of digestion-inhibiting compounds. Ecologists generally differentiate between hydrolyzable (low molecular weight) tannins and condensed (high molecular weight) tannins, which commonly occur together in the foliage of woody angiosperms (Bernays, 1981). Useful overviews of tannin types and the problems they can pose to herbivores have been published by Mehansho *et al.* (1987), Bernays *et al.* (1989), Lee *et al.* (1991), and McArthur *et al.* (1991). Waterman and Kool (1995) summarized what is known about colobine food selection with regard to secondary compounds, including tannins.

On occasion, analytic data show that wild primates eat plant parts with higher concentrations of tannins or other secondary compounds than those in plant foods that they ignore (Milton, 1979; Davies *et al.*, 1988; Dasilva, 1994; Maisels *et al.*, 1994). Such foods may also contain more protein or other nutrients than ignored foods, suggesting that animals may at times be willing to ingest foods with a somewhat higher tannin content if they can net a higher nutrient return (Freeland and Janzen, 1974; McKey, 1978; Maisels *et al.*, 1994). The accumulation of tannins in plant tissues is often associated with other plant characteristics with proven disadvantages to feeders such as a low water and protein content (Bernays, 1981). Thus primates may be avoiding many plant parts in the habitat not because of digestion-inhibiting secondary compounds but because, in general, such foods are not worth eating (Milton, 1979).

In vitro, condensed tannins complex with dietary protein, an activity that could reduce protein digestibility *in vivo* (Feeny, 1969; McArthur *et al.*, 1991). However, the mouth and digestive tract of living animals do not necessarily approximate conditions *in vitro*, and postingestional effects of tannins on food digestion in primates are unknown. Many primate species, particularly leaf-eaters, might have features that buffer them from lowered digestibility as a result of condensed tannins. These features may include proline-rich proteins in saliva and a neutral or high pH in the mouth or gut or both.

Salivary Glands

Mehansho *et al.* (1987) found proline-rich proteins (PRPs) in the saliva of various mammalian species, including humans. These proteins have a high affinity for tannins and can reverse the detrimental effects of tannins in the diets of rats and mice (Mehansho *et al.*, 1987). Proline-rich proteins constitute about 70% of the proteins in human salivary secretions. Similar proteins can be dramatically increased or induced in the parotid and submandibular glands of various rodents—rats, mice—by isoproterenol treatment (Mehansho *et al.*, 1987). Feeding tannins to rodents mimics the effects of isoproterenol injections, suggesting that the primary role of PRPs is to bind polyphenolic compounds such as tannins (Mehansho *et al.*, 1987). The presence of PRPs in saliva of mammals as distinct as mice and humans suggests that PRPs may be fairly ubiquitous salivary constituents. However, some ruminant browsers, e.g., domesticated goats, do not secrete PRPs (McArthur *et al.*, 1993; see also Foley and McArthur, 1994), suggesting caution in attributing them to leaf-eating primates without supporting data.

High pH has also been suggested to lower digestion-inhibiting effects by tannins by reducing the formation of tannin-protein complexes (Fox and

Macauley, 1977). Copious amounts of alkaline saliva in the mouth of the feeder contact tannins on ingestion and, when swallowed, in the case of foregut fermentors, may raise the stomach pH, thereby further inhibiting the formation of tannin–protein complexes.

Howlers and colobines are characterized by hypertrophied salivary glands, particularly the parotids (Hill, 1972; Milton, 1977; Bauchop, 1978; Kay and Davies, 1995). Ruminants likewise have hypertrophied salivary glands, particularly the parotids, which typically are largest in browsers (Robbins *et al.,* 1995). In grazing ruminants such as cattle, large salivary glands help to maintain a neutral pH in fermentative sections of the foregut (Van Soest, 1982; Robbins *et al.,* 1995), and in both ruminants and macropodines, saliva is an important source of phosphorous for the symbiotic bacteria in the forestomach (Hume, 1982). In ruminant browsers, however, large salivary glands appear to function largely to counter plant chemical defenses (Robbins *et al.,* 1995).

Like ruminant browsers, colobines eat leaves of woody angiosperms rather than forbs. Thus, by analogy, one might predict that unusually large salivary glands in colobines likewise function to counter plant chemical defenses, particularly tannins (Kay and Davies, 1995). This interpretation is strengthened by the fact that howlers have large salivary glands (Hill, 1972) and do not have a fermentative foregut. In howlers, large salivary glands probably function to neutralize tannins in wild foods instead of buffering the stomach pH. Saliva of *Alouatta* spp. and the Colobinae probably is rich in PRPs (Cork and Foley, 1991; Waterman and Kool, 1995; Kay and Davies, 1995).

Tannins, at least up to certain concentrations, are probably not effective feeding deterrents for many mammals (Cooper and Owen-Smith, 1985; Bernays *et al.,* 1989; McArthur *et al.,* 1993; Maisels *et al.,* 1994; Waterman and Kool, 1995). Nontannin phenolics—toxins—rather than condensed tannins appear to constrain intake in some ruminant browsers (McArthur *et al.,* 1993). Rats fed dietary tannin show a high fecal nitrogen excretion, but it is primarily endogenous instead of dietary and results largely from mucus hypersecretion or enzymatic activities or both (Glick and Joslyn, 1970; Mitjavila, 1977). High tannin concentrations, however, can result in food avoidance or even death, depending on the animal species, the tannin level, and the quantity of tannin-rich foods ingested.

Using terminology derived for ruminants, colobines have been referred to as concentrate feeders (Kay and Davies, 1995). But Robbins *et al.* (1995) pointed out that the tree and shrub leaves consumed by ruminant browsers are not actually concentrates since they are heavily defended by soluble secondary plant compounds, a condition equally or more likely for many foods of colobines. Accordingly, the term concentrate feeder may need to be reconsidered for colobines (Cork, 1994; Gordon and Illius, 1994).

PHYSIOLOGICAL ECOLOGY OF FOOD SELECTION

Little is known about physiological cues involved in food selection by wild monkeys. Young howlers (*Alouatta palliata*) may acquire information about edible leaf species by observing the mother or another howler eat a particular leaf and then sampling it themselves; fruits apparently are sampled and learned largely as a result of social facilitation (Whitehead, 1993). E. Gale (personal communication), who raised abandoned infant howlers (*Alouatta palliata*) in her home in Panama, reported that young monkeys would accept novel foods such as spinach only after she had first masticated the leaves and then let the monkey sniff her mouth.

Temporarily caged and hungry wild howlers in Panama were offered leaves of *Ficus insipida* of different ages (Milton, 1984); young leaves of this species are a highly preferred howler food at this site (Milton, 1980). Monkeys would glance rapidly at, sniff, and then immediately eat or reject the offered leaf. Similar staring and sniffing behavior occurred in several captive *Hapalemur griseus* presented with bamboo foliage at the Duke University Primate Center (Milton, 1978b). Chemical analysis showed that leaves of the age accepted and eaten by howlers had a higher protein–fiber ratio than the leaves that they rejected. Given the behavior of the monkeys, it seems possible that visual or olfactory cues could convey information to monkeys about leaf quality. However, there could also be other factors that influenced the pattern of leaf choice observed in these trials.

Howlers and other primates that forage as a cohesive social unit must be able to make an immediate individual assessment of the quality of potential foods since foliage and fruits from particular trees, e.g., lower vs higher part of tree, shady vs sunny part of tree, or different trees of the same species can differ in nutritive value (Glander, 1978, 1982; Howe, 1983; Mole and Waterman, 1987). Within a given tree, conspecific cueing, other than mother to dependent offspring, might not be an effective tactic because, at least in the case of howlers, individuals scatter rapidly within the canopy of particular food trees, each monkey presumably trying to feed in the highest-quality food patch it can access for every food source visited. It is possible that monkeys may array themselves within a food tree in relation to kinship or dominance rankings, with closer kin of higher-ranking animals getting the best feeding sites.

Cues involved in food selection is an area that has been little studied by primatologists (but see Snodderly, 1978; Janson, 1983: color vision studies; Simmen, 1994; Laska *et al.,* 1996; Laska, 1996: sugar threshold detection studies). Such research would prove useful in enhancing our understanding of features which underlie the patterns of food choice documented in the natural environment and could aid in a better understanding of niche partitioning between sympatric species.

OVERVIEW

Howlers and colobines are assumed to have the same basic nutritional requirements as other primates. Yet in terms of diet, these taxa stand out from most other primates in the extent of their dependence on leaves as food. Because mature leaves are virtually omnipresent in tropical forests and young leaves also tend to be far more abundant in space and time than flowers or green or ripe fruits (Milton, 1980), it would seem that, all else being equal, other primates too would eat more leaves if this were possible. As they do not, we must assume that, for whatever reason, leaf eating is not a viable dietary option for them.

Clemens (1980) noted that although we often assume that certain conditions must be fulfilled for fermentative digestion to occur in a given animal species, available data suggest that comparable activities take place within the digestive tract of many nonruminant herbivores, omnivores, and carnivores as well as birds (Sakata, 1994). The difference between taxa must therefore relate to their degree of reliance on gut microorganisms and fermentation to meet energetic and nutritional needs and the morphological, physiological, and behavioral adaptations associated with this process. Howlers and colobines appear to have an obligate commitment to a digestive strategy predicated on fermentation and their food choices presumably reflect this commitment. Though plant-eating animals are often viewed as having relatively simple dietary requirements, e.g., grass or leaves, in fact the opposite is generally the case (Johnson, 1966). Both howlers and colobines are likely to require fairly specific, though somewhat different, types of foods for maximal digestive efficiency and their respective food choices should reflect these digestive constraints. For this reason, the postulated dietary breadth of colobines as well as the flexibility of the colobine digestive system are likely to prove largely illusory (Dasilva, 1994; Kay and Davies, 1995).

Though howlers and colobines both depend on fermentative processes, their major sites of fermentation are in different sections of the gut and should constrain their holders to somewhat different patterns of food selection. Howlers can eat considerable amounts of ripe, sugary fruit as well as leaves each day; however, as foods eaten by howlers apparently must provide them with high-quality protein and energy, they must be careful to select foods that will meet this nutritional demand. Colobines, in contrast, appear limited in their ability to utilize ripe, sugary fruits and presumably sacrifice most dietary protein to gut flora. But colobines apparently are also able to depend more heavily on large quantities of mature foliage, and, in some species, digestible seeds, in the diet than howlers are. Both taxa, however, apparently rely to an important—obligate—degree on energy derived from short-chain fatty acids to meet a major portion of their daily energetic requirements. Colobines appear to have a higher digestive efficiency with respect to NDF than that of howlers and, in addition, presumably derive considerable high-quality protein from gut flora.

The utilization of short-chain fatty acids as immediate energy sources, whether an obligatory or facultative process, has a basic effect on an animal's performance in both nature and efficiency and undoubtedly bears a direct relation to the endocrinological control of energy metabolism (Johnson, 1966). Considerably more attention needs to be devoted to the degree of dependence on VFAs in these two primate taxa and whether VFA production and absorption tend to approximate a more or less steady state or vary on either a short-term or a seasonal basis (Sakata, 1994).

Investigation of metabolism and nutrition in animals with dependence on a fermentation strategy is also complicated by the presence of two entirely separate metabolic systems—host and microbes—which, though influenced by each other in some ways, can also vary independently (Johnson, 1966). Furthermore, even when the sites and approximate rates of VFA production and the pattern of digestive kinetics are known for particular primate species, this is still no guarantee that their digestive strategy and food choices in the natural environment will be understood (Clemens and Phillips, 1980). The study of physiological ecology offers no quick fix in terms of an immediate understanding of the intricacies of primate food choice in the natural environment, but it provides an approach that can enhance investigation of this topic and holds the promise that, eventually, some satisfactory answers to our questions will be forthcoming.

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