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The Role of Food-Processing Factors in Primate Food Choice

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MOST PRIMATES are strongly dependent on plant foods. Field studies show that primates do not feed on plant parts at random but rather have decided food preferences (Casimir 1975; Hladik 1977; Oates et al. 1977, 1980). The food choices of primates have generally been attributed to one of two principal factors: the nutritional and/or toxic content of the particular plant part or its relative availability in space or time (Hladik and Hladik 1969; Casimir 1975; Glander 1978; McKey et al. 1978; Milton 1979; Oates et al. 1980). It has also been suggested that body size may influence primate food choice (Hladik 1978; Gaulin 1979; Milton 1980). Though each of these factors would appear to play some role in determining primate food choice, very often sympatric plant-eating

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primate species of approximately the same adult body size show quite different patterns of food choice (Hladik and Hladik 1969; Clutton-Brock 1974; Hladik 1977; Sussman 1979; Milton 1981). At times a particular food appears hyperabundant, indicating that immediate competition for it may not be an issue. In such cases, none of the above factors, either singly or in combination, is sufficient to explain the feeding patterns observed. This strongly suggests that other factors are also important.

In examining factors related to food choice, the ecological literature has tended to focus primarily on features of external morphology. In birds, for example, food choice has been correlated with such features as body or bill size, and similar explanations have been suggested for food choices of fish and reptiles (Schoener 1965; Hespenheide 1971, 1975; Ricklefs 1972; Werner 1977). Most such studies, however, have examined food choices of secondary rather than primary consumers. Features of external morphology may well be of critical importance to secondary consumers since their items of diet, animal prey, are generally mobile and often protected by external defensive features such as spines or claws. Secondary consumers may therefore require corresponding features of external morphology to cope efficiently with the escapist or defensive tactics of particular prey types. As primary consumers eating sessile plant parts, primates face many problems quite different from those faced by secondary consumers. These problems would appear to call for somewhat different adaptive solutions.

Plant Defenses

In large part, the problems faced by plant-eating primates have to do with the types of defenses plants employ to protect their potentially edible parts from predation. Such defenses can be quite elaborate and range through several levels of organization; generally, plants employ several levels of defense simultaneously. The first level of defense may be mechanical. Mechanical defenses can include such things as thorns, spines, hairs, or hard seed coats; they can also include the height at which the potentially edible item, or the branching structure supporting the item, is found. Most such external defenses appear to pose little problem to primates (Milton, personal observation). The second line of defense can be the manner in which potentially edible parts are deployed in space and time. The low individual densities characteristic of many tropical tree species and their varied phenological patterns can function, at least in part, to lower predation on leaves, flowers, or unripe fruits (Janzen 1970; Milton 1980). The single most important defense employed by plants, however, would appear to be the chemical composition of the plant parts themselves. It is this third level of chemical protection that appears to be the most ubiquitous plant defensive strategy. Under the term *chemical composition* I include the nutritional content of the plant or plant part, its proportion of indigestible material, and its content of presumably defensive compounds such as phenolics or alkaloids. To appreciate better how these chemical features might function to deter primary consumers, it is useful to take a closer look at some of the problems associated with each.

Nutrient Content

Unlike many foods from the second trophic level, foods from the first trophic level show considerable variability in nutrient content. For example, leaves, particularly young leaves, may contain considerable protein but are usually low in ready energy (Milton 1979, 1981). Conversely, ripe fruit tends to be high in ready energy but notably low in protein (Hladik and Hladik 1969; Milton 1981). Flowers of particular species may be quite nutritious but, as a food category, show considerably more interspecific variability in nutritional content than either leaves or fruit (Milton 1980). Many primates must choose foods from more than one dietary category each day to get the balance of essential nutrients and energy they require. This in turn limits the amount of food that can be eaten from any one category per unit time. Potential nutrient imbalance is a real and persistent problem for many primary consumers and one that is generally foreign to secondary consumers (Maynard and Loosli 1969; Westoby 1974). This is not to imply that nutrient allocation patterns in plant parts reflect herbivore defenses. But the nutrient imbalance characteristic of most plant foods nonetheless poses a dietary problem for primary consumers that must somehow be overcome.

Indigestible Materials

A second major problem with plant foods, and one that deserves further study, is the fact that most plant parts are high in indigestible cell wall material. Plant cell walls are made up primarily of cellulose, hemicelluloses, and lignin. These three cell wall constituents are impervious to all known digestive enzymes of vertebrates. Thus the more cell wall material a primate eats, the more indigestible bulk is being passed through the digestive tract, and this material, in the absence of certain mitigating factors, provides no nutritional benefits to the feeder (Moir 1967; Parra 1978). Apparently in response to this problem, many plant-eating animals have enlarged sections in the gut that harbor vast colonies of bacterial flora with cellulolytic properties. This gut flora can degrade the cellulose and hemicelluloses (structural carbohydrates) of plant cell walls by fermentation. During fermentation various end products are produced, including energy-rich short-chain fatty acids (VFAs). These fatty acids can often be absorbed by the host and may make an important contribution to its energy budget (Bauchop and Martucci 1968; Parra 1978). In the absence of sufficient gut flora, however, animals eating diets high in cell wall material, particularly highly lignified material, apparently derive little nutritive or energetic benefit from passing this material through the gut.

The leaves eaten by primates are generally high in cell wall material. Some 30% to more than 50% of the dry weight of a given leaf may be made up of cell walls (Milton 1979). Therefore, we might predict that primates deriving an important part of the diet from leaves should show adaptations either to facilitate fermentation or to move indigestible matter rapidly through the gut.

Fruit, too, can be extremely high in indigestible material. This is because most edible fruit pulp is elaborated by trees to serve as a lure for seed-dispersal agents. Tree species have many techniques

for ensuring that fruit-eating animals actually will disperse seeds away from the parent tree. Often nutrients adhere so tightly to the seed that it seems most efficient for the feeder to swallow the entire fruit—skin, seeds, and pulp—and digest off the pulp (e.g., *Spondias mombin; Doliocarpus* spp.). In other cases, seeds are so minute or so thoroughly mixed with the edible pulp that it seems most expedient to swallow the entire fruit rather than try to pick out the indigestible material (*Ficus* spp.; *Hyeronima laxiflora;* Milton, personal observation). In both cases, however, the feeder is filling up on seeds, as well as pulp, and, unlike leaves, seeds generally are not broken down by digestive enzymes or bacteria in the gut and are excreted intact (Hladik and Hladik 1969; Milton personal observation). Thus fruit-eating primates, whose foods typically contain seeds that are swallowed, should have some means of dealing with indigestible material such that it is passed from the gut as rapidly as possible once digestible nutrients have been removed from the seed surface. This poses an interesting paradox for primates eating both fruits and leaves since fruits, because of the seeds, would appear to call for relatively rapid food passage rates whereas the latter would be most efficiently digested with slow food passage rates (Milton 1981, and below).

Secondary Compounds

All plant parts contain the chemical constituents known as secondary compounds, some of which may function to deter plant-eating animals (Feeny 1971; Freeland and Janzen 1974; Ryan and Green 1974; McKey et al. 1978; Oates et al. 1980). Some secondary compounds are distasteful or malodorous; others can interfere with the digestion of nutrients in the gut or with the metabolic processes of the feeder, at times with fatal results (Freeland and Janzen 1974; Glander 1975). There is a vast and rapidly growing literature on the possible interrelationships between secondary compounds and primary consumers, but as yet there is no general consensus about the role of these substances in plant defense.

Few data are available on the role of secondary compounds in determining patterns of primate food choice. Available data suggest that in some cases such compounds do not exert any notable influence in food selection whereas in others they may well be of considerable importance (Glander 1975, 1978; Hladik 1977; Milton 1979; Oates et al. 1980). *In vitro* experiments show that leaf tannins present in species eaten by primates can bind with protein and lower digestive efficiency. If similar conditions exist *in vivo,* this too could influence food selection patterns (McKey et al. 1978; Milton et al. 1980; Waterman et al. 1980).

Solutions to Chemical Problems

Since many principal defenses of plants are chemical, they are internal to the plant or plant part whereas the principal defenses of foods from the second trophic level tend to be morphological and external. We might therefore expect that primary consumers, in contrast to many secondary consumers, have been under strong selective pressure with respect to the development of features of internal morphology particularly well suited to deal with the primarily internal defenses of their principal items of diet. In particular, the morphology of the gut is expected to show adaptations serving to counteract or resolve many of the nutritional and other chemical problems characteristic of plant foods. Such adaptations, in turn, are likely to play an important role in food choice by permitting particular primate species to specialize on some subset of the total range of plant resources. This could lower foraging costs associated with selective feeding on patchily distributed plant foods or facilitate use of more abundant plant foods high in fiber (e.g., mature leaves). It could also help to ameliorate possible competition between sympatic primate species eating plant-based diets.

In order to appreciate why the morphology of the gut might help to resolve some of the chemical problems inherent in most plant foods, it is useful to understand some aspects of the digestive process. The digestibility of food depends on two principal factors, namely, digestive rate and the amount of time food can remain in the digestive tract. The amount of time food remains in the digestive tract is determined by the passage rate of digesta and the capacity of

the digestive rate (Van Soest 1977). This relationship can be expressed in a simplified fashion by the equation: $D = r_d\,(L/r_p)$ where D is digestibility, r_d is rate of absorption per unit area of gut, L is gut length, and r_p is passage rate for digesta in some unit such as millimeters per minute. Thus overall digestibility of a given meal is affected by the interaction between the amount of time food can remain in the digestive tract and the passage rate of food. In effect, these two factors represent opposite points on a continuum, and animal species can be ranked along this continuum, depending on whether they tend to maximize the efficiency of digestion or the volume of food processed per unit time (Bell 1971; Parra 1978; Milton 1981). Animals that pass food through the gut relatively slowly for their body mass presumably have adopted a solution emphasizing maximal nutrient extraction from each meal. In particular, we might expect such animals to show adaptations in the digestive tract for the efficient fermentation of plant cell wall material, which is generally a time-consuming process. Conversely, animals passing food through the gut relatively rapidly for their body mass might be feeding on a resource base that is generally of poor quality or low in one or more essential nutrients. Fruit would fall into this latter category since it tends to be high in nonstructural carbohydrates and low in protein. By passing large quantities of low-quality or imbalanced foods rapidly through the gut, such animals should be able to extract an adequate and balanced diet.

Therefore, a knowledge of the food passage rate characteristic of a given species can give insight into the type of foods the animal is best able to process and help to explain its pattern of food choice.

To investigate the role of gut morphology in primate food choice, I carried out a series of feeding experiments to determine food passage rates of two neotropical primate species, howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*). Howler monkeys and spider monkeys occur sympatrically over much of their very wide geographical range, are approximately the same adult body size, and feed exclusively on foods from the first trophic level. Thus they are good subjects for an examination of this nature.

Feeding trials showed that howler monkeys, which eat considerable foliage, retained food in the digestive tract for a significantly longer time than spider monkeys (Milton 1981). As discussed above, leaves tend to be high in cell wall material, but if food passage rates are sufficiently slow and adequate numbers of cellulolytic gut flora are present, the structural carbohydrates in leaves can provide energy for the feeder indirectly. Data show that considerable cell wall material is degraded in the hindgut of howlers and indicate that some of the fatty acids produced in fermentation are absorbed (Milton et al. 1980; Milton and McBee 1982). In contrast, spider monkeys, which are strongly frugivorous at all times, turned over gut contents very rapidly. Mean time of first appearance (TFA) of markers in spider monkeys was 4.4 ± 1.5 h compared with 20.4 ± 3.5 h in howlers. This fast food passage permits spider monkeys to rid the gut rapidly of indigestible seeds present in fruit, their principal dietary item. Further, by turning over a large volume of fruit each day, they are apparently able to compensate for the low protein content of such foods.

The stomach, small intestine, and cecum of these two species are roughly similar in relative surface areas (Hladik 1967; Milton 1981), but colons of howlers have approximately double the capacity of those of spider monkeys. In effect, it would appear that each species is living on a diet that is not tenable for the other owing to differences in gut proportions and food passage rates. On a primarily fruit diet of the type eaten by spider monkeys, howlers with their voluminous colons and slow food passage rates presumably would not be able to meet their demands for protein. On the other hand, on a primarily folivorous diet of the type eaten by howlers, spider monkeys, with their relatively short narrow colons and fast food passage rates presumably would not be able to meet demands for energy. Thus gut morphology and food passage rates, in conjunction with other aspects of behavior and morphology characteristic of each species, appear to limit food choice so that each species is best nourished when eating a particular subset of the available plant resources. Further details of these experiments are found in Milton 1981.

These results suggested that similar features of gut morphology, as well as other factors related to food-processing efficiency, might also limit food choices by other primate species. To investigate this possibility I carried out the series of feeding experiments described next.

Feeding Experiments

In these experiments, individuals of 14 primate species were fed colored markers to obtain an estimate of food passage rates. Relevant data on all study subjects are presented in table 9.1. New World species were tested in the Republic of Panama at the Gorgas Memorial Laboratory, and at the Smithsonian Tropical Research Institute on Barro Colorado Island, and in Brazil at the Jardim Zoologico in São Paulo and the INCAP Jardim Zoologico in Manaus. Apes were tested at the San Francisco Zoo. Three human subjects also volunteered to eat markers to provide a data point for *Homo sapiens*.

Methods

Small colored plastic markers (about 4 mm wide, 1 mm thick) were concealed in foods offered to subjects. Subjects differed in the number of markers swallowed, but all animals listed in table 9.1 consumed enough markers that it appeared worthwhile to monitor fecal material for time of first appearance of markers. Either directly before or immediately after markers were swallowed, animals were fed their principal meal of the day, which in all cases consisted of a variety of fresh fruits, some leafy material such as lettuce, bread, generally soaked in milk and vitamins, and in a few cases pieces of commercial monkey chow. My objective was to get markers into the stomach along with a large, fresh bolus of food, since mixing in the stomach should distribute markers through the food. The time of first appearance of markers and the number of markers present in each set of feces could then be used to estimate the passage time of that meal.

There are a number of difficulties in using markers to estimate food passage rates (Alvarez and Freedlander 1924; Wiggins and Cummings 1976). Even under ideal conditions, using soluble and particulate markers simultaneously, it can be difficult to interpret the biological significance of data obtained. Since in these experiments all animals ate the same type of markers and approximately the same type of foods, data should be comparable, at least in rela-

Table 9.1. Time of First Appearance of Markers in Fourteen Primate Species

Species	No. Individuals, Sex and Age	Est. Mean Body Wt. (kg)[a]	No. Trials per Subject	Time of Feeding of Markers	No. of Hours for Time of First Appearance of Markers	Range of TFAs (when n = >1)
Cebus capucinus	3 AM[b]	3.0	2	0800; 1400	$\bar{X}$ = 3.5	3.0–5.5
Cebus apella	1 AM	3.5	2	0800; 1400	3.5	
Pithecia monachus	1 AF	1.9	1	0900	20.0	
Chiropotes albinasa	1 AM, 1 SAM	3.0	1	0930	5.0	See text
Cacajao calvus	1 AM, 1 AF	3.0	1	0945	5.0	See text
Alouatta palliata	2 AM, 1 AF, 1 JF	6.9	[c]	0800; 1630	$\bar{X}$ = 20.4	16–23
Ateles geoffroyi	1 AM, 6 AF, 2 JF	7.6	[c]	0800; 1400	$\bar{X}$ = 4.4	2.75–7.75
Ateles paniscus	2 AM, 2 AF	7.8	1	1030	$\bar{X}$ = 5.25	5.0–5.5
Lagothrix lagotricha	2 AM, 1 SAF	6.5	1	1000	$\bar{X}$ = 6.75	6.5–7.0
Brachyteles arachnoides	1 AF	12.0	1	0900	8.0	
Pan troglodytes	3 AF	45.0	1	1600	36–38	See text
Pongo pygmaeus	1 AM, 1 AF	53.0	1	1600	36–38	36–38
Gorilla gorilla	1 AF, 1 JM	103.0	1	1600	36–38	See text
Homo sapiens	1 AF, 2 AM	$\bar{X}$ 67 ± 8.7	1	0730	26 ± 1.0	25–27

[a] Sources for weights as follows: All Pithecinae, *Cebus apella*, and *Ateles paniscus* from Fleagle and Mittermeier (1981) or Mittermeier, personal communication; *Alouatta palliata* from Milton, based on actual wts. of study subjects; *Ateles geoffroyi* from Querling (1950); *Lagothrix* and *Cebus capucinus* from Napier and Napier (1969); *Pan* and *Pongo* from Clutton-Brock and Harvey (1977). *Brachyteles*, female gorilla, and *Homo sapiens*, actual weights of study subjects. Juvenile gorilla, wt. = ca. 46 kg.

[b] A = adult; M = male; F = female; S = subadult; J = juvenile.

[c] Variable, see Milton (1981) for complete details.

tive terms. In my opinion these markers probably move through the gut in the same manner as indigestible food particles such as seed coats.

Once markers and food were swallowed, animals were checked at regular intervals to see if defecation had occurred. When feces appeared, the time was recorded and fecal material was examined for presence and quantity of markers. All primate facilities except Barro Colorado Island closed at 1700–1800 h and did not reopen until 0800 the following day. Therefore, during these hours animals could not be monitored. Time of first appearance of marker material in feces produced during this period could only be estimated based on appearance of the fecal matter. Because of this lack of continuity, data vary in quality. In some cases I was present when the first marker material was passed; in other cases, estimates are accurate to within 15 min; in other cases, TFA is simply a best estimate. When presenting results below, I give my opinion of the accuracy of the data. Further, though TFA in most cases is believed to be a good estimate, data from these trials cannot be used to indicate precisely how much food was passed through the tract per unit time; the data indicate only when markers first began to pass out of the tract and, in some cases, the percentage of marker material present. Moreover, animals were not fed natural diets. These results might change somewhat under free-ranging conditions owing to differences in the digestibility of wild foods or to different activity and feeding regimes of free-ranging animals.

Results

New World Monkeys

Cebus capucinus Animals ate good quantities of markers and food and were closely observed. Time of first appearance of markers averaged 3.5 h. Many markers were passed within 8 h after ingestion, but some were still appearing in the feces in small amounts 24 h later.

Cebus apella This animal ate good quantities of markers and food and was closely observed. Time of first appearance was 3.5 h. Many markers were passed within 8 h after ingestion, but some were still appearing in the feces in small amounts 24 h later.

Pithecia monarchus This animal ate moderate amounts of markers and food and was very closely observed during the first 8 h after ingestion during which time it is certain that no markers were passed. By 0800 the following day (approximately 23 h after the initial feeding), this animal had passed many markers. Feces containing markers appeared very fresh, and I estimate their passage at around daybreak (0530–0730). Time of first appearance in this animal is therefore placed at ca. 20 h. More fecal material containing markers was passed in my presence at 0800. The fecal material was produced in small pellets similar in appearance to those of a rabbit or goat.

Chiropotes albinasa Results of trials on both *Chiropotes* should be regarded as tentative. The adult male swallowed only three pieces of marker material and ate little food. Food passage rates were probably quite depressed. No markers were produced during the first 8 h of observation. One marker was recovered in feces at 0800 the following day and appeared to have been passed in ca. 20 h.

The subadult *Chiropotes* ate good quantities of both markers and food. Time of first appearance in this animal was ca. 5 h after ingestion and a considerable amount of marker material was passed within 8 h after ingestion. This animal had slightly liquid feces, however, and passage may therefore have been speeded up. Since conditions were not entirely normal in either case, results are inconclusive. Estimates from the subadult are believed to be more accurate because the animal did eat considerable marker material and food, and many markers were recoverd.

Cacajao calvus Each animal ate a moderate quantity of markers and food. Time of first appearance in both was ca. 5 h after ingestion, and a considerable amount of marker material was passed within 8 h after ingestion.

Alouatta palliata Animals ate good quantities of markers and food and were very well observed. Time of first appearance averaged 20.4 h—about 23 h if fed to animals before noon and about 16 h if fed after noon. Most markers were excreted within 30+ h after ingestion, but a few were still appearing in feces 72 h after the initial feeding. (See Milton [1981] for details of these feeding trials.)

Ateles geoffroyi Animals ate good quantities of markers and food and were very well observed. Time of first appearance averaged 4.4 h with a range of from 2.75 to 7.75 h. Most markers appeared to be excreted within 8+ h after ingestion but a few were still appearing in the feces more than 24 h after the initial feeding. (See Milton [1981] for details of these feeding trials.)

Ateles paniscus Animals ate good quantities of markers and food and were very well observed. Time of first appearance averaged 5.25 h. Most markers appeared to be excreted within 8+ h after ingestion.

Lagothrix lagotricha Animals ate good quantities of markers and food and were well observed. Time of first appearance averaged 6.75 h. More markers were seen in feces the following morning, ca. 22 h after the initial feeding.

Brachyteles arachnoides This adult female ate good quantities of food and markers and was very well observed. Time of first appearance was exactly 8 hours after ingestion. Considerably more marker material was seen in fecal material the following morning, presumably passed some 20–23 h after the initial feeding. A second experiment was carried out on this animal, but results could not be used, for she developed severe diarrhea with greatly accelerated passage rates that were decidedly abnormal.

Apes

All apes ate generous quantities of markers (ca. 150 each) and food and were well observed during daylight hours.

Pan troglodytes Good data are available for three adult females. One had a TFA of ca. 15 h, producing three markers in one set of feces. The first notable appearance of markers, however, occurred in this female around 36–38 h after ingestion. The other two females had

TFA's of around 36–38 h and produced many markers (25%) at this time.

Pongo pygmaeus The two adult orangs appeared to have approximately the same TFA, estimated at 36–38 h after ingestion. As for two of the three chimpanzees, TFA of markers occurred with the appearance of considerable (15%–25% of total) marker material.

Gorilla gorilla Markers were initially fed to five gorillas, but owing to logistical problems, accurate data could be collected only for two, a juvenile male and an adult female. The juvenile male had a TFA of ca. 17 h, producing two markers at this time in one set of feces. The first notable passage of marker material (ca. 25% of total) in this animal occurred approximately 36–38 h after ingestion. The adult female had a TFA of approximately 36–38 h and passed around 18% of the markers at this time. More than 84 h after the initial feeding, markers were still appearing in small amounts in her feces, as well as in those of two other adult animals whose passage rates could not be carefully monitored. This adult female and one other adult were observed to practice coprophagy (one incident for each animal) and one juvenile ingested feces of one adult female (one incident).

Homo sapiens The three human subjects, two adult men and one adult woman, swallowed 150 markers each along with considerable food and were very well observed. Time of first appearance averaged 26 h ± 1 h. As was characteristic of the Pongidae, considerable marker material was excreted at this time (33% of total in two male subjects, 10% in the female subject). In a series of detailed experiments on human transit times using glass beads as markers, Alvarez and Freedlander (1924) found that the average subject passed 15% of the beads within 24 h after ingestion, 40% within 48 h and 75%–80% within 96 h. Then days or even weeks could elapse before the remaining 20% were all finally recovered.

Discussion

Field studies show that different primate species often feed on different subsets of the available plant resources, but reasons for these species-specific patterns of food choice are not always apparent. It was suggested that features of gut morphology (and its effects on food passage rates), and other factors related to food-processing efficiency, might play an important role in determining what subset of plant foods a given primate species finds most suitable, i.e., that food choice might be dictated as much by internal constraints intrinsic to the digestive "strategy" of the feeder as by extrinsic factors such as nutrient content or relative availability.

Data on food passage rates show that smaller bodied species tend to pass food through the gut more rapidly than larger bodied species (fig. 9.1). Mehrtens (1971), in working with food transit times in ruminants, found that body size was the single variable showing the highest (negative) correlation with food passage rates. There seems

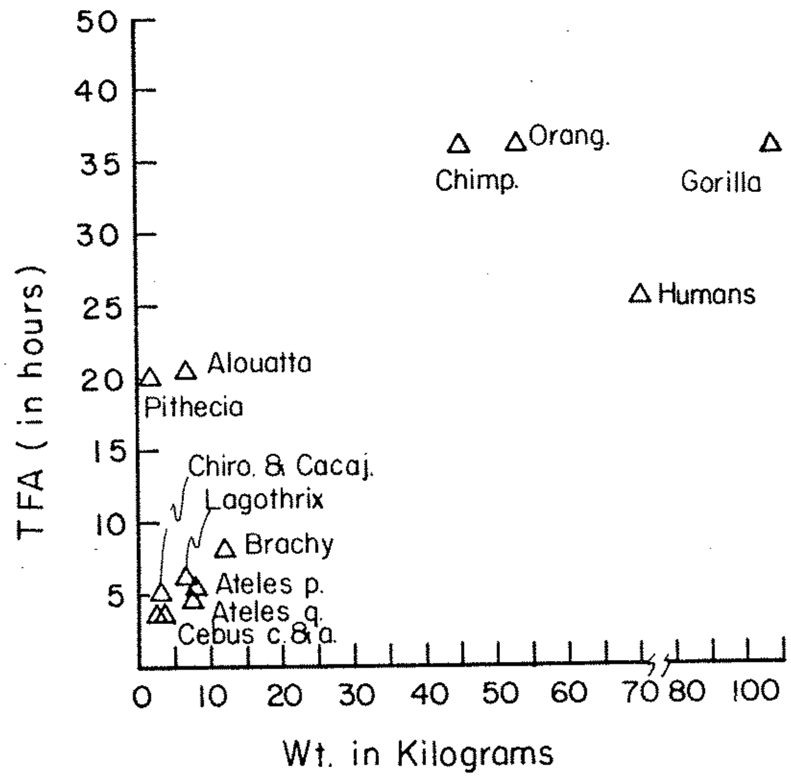

Figure 9.1. Time of first appearance of markers plotted against body weight for 14 primate species.

to be good physiological reason why smaller species should generally show faster food transit times. As pointed out by Parra (1978), as body size increases, metabolic costs per unit body weight decrease exponentially, while gut volume remains proportionate to body mass (see also Hungate et al. 1959). This implies that smaller homeotherms have disproportionately high energetic costs per unit body weight but no "extra" room in the gut to process a proportionately greater amount of food. One solution to this rather paradoxical problem is for smaller animals to turn over gut contents more rapidly than their larger counterparts (Hungate et al. 1959; Parra 1978). This fact helps to explain why smaller primate species generally seek out low-fiber, nutritionally concentrated resources, amenable to rapid digestion (Hladik 1977; Gaulin 1979).

Data show that of the smaller species examined, all except *Pithecia* had TFAs of 3.5 to 5 h and excreted considerable marker material within 8 h after ingestion. Field data show that all of these species except *Pithecia* avoid leaves as food (Fooden 1964; Oppenheimer 1968; Roosmalen, Mittermeier, and Milton 1980; Fleagle and Mittermeier 1981; Happel, 1981). The two *Cebus* species eat fruits and seeds from the first trophic level and insects and small vertebrates from the second (Oppenheimer 1968; Hladik and Hladik 1969; Milton, personal observation). The manual dexterity of this genus may have developed, at least in part, in association with its dietary habit of unrolling dead leaves to look for insect prey (personal observation).

Chiropotes is an unusual primate for its body size. It is generally reported to take all of its diet from the first trophic level, although Ayres and Nessimian (1982) indicate some use of food from the second trophic level. First-level foods reported for *Chiropotes* are fruit pulp, and immature and mature seeds, particularly those from members of the Lecythidaceae (Brazil nut family) and Bigoniaceae (Roosmalen et al. 1980; Ayres, personal communication). Such seeds can be a rich source of oils and protein and are low in indigestible bulk.

No data are available on the natural diet of *Cacajao*, but its food passage rates and dental morphology are similar to those of *Chiropotes*, suggesting that this genus may exploit a similar diet. Data are available on the relative surface area of different sections of the gut for most of these smaller species (including *Pithecia*); these show that the small intestine has by far the greatest relative surface area and that other sections of the gut are not notable in volume (Fooden 1964; Hladik 1967; Chivers and Hladik 1980). A well-developed small intestine is consistent with a diet of high-quality, volumetrically concentrated food resources, calling for a digestive strategy facilitating the rapid absorption of nutrients without the need for prolonged retention of food in other sections of the digestive tract.

The one *Pithecia* used in the trials had a strikingly long TFA in comparison with most other species tested. If future work confirms that long retention time is characteristic of the genus, *Pithecia* would appear to have a digestive strategy considerably different than those of other members of the Pithecinae or the *Cebus* species. The pelleted appearance of the feces also suggests a different strategy with respect to nutrient extraction. Data from Fooden (1964) suggest that *Pithecia* may show some reduction in the size of the small intestine and some increase in the size in the colon when compared with *Chiropotes chiropotes*. Free-ranging animals are reported to eat fruits of trees and vines (Fleagle and Mittermeier 1981). Happel (1981) noted fruit-eating in her observations of free-ranging animals but also commented on the fact that animals spent 16% of total feeding time eating leaves. In this context, it is interesting to note that *Pithecia* occurs sympatrically with both *Chiropotes* and *Cacajao*, but that members of the latter two genera do not appear to show geographical overlap (Mittermeier, personal communication; Ayres, personal communication). A different digestive strategy implies a different pattern of feeding that could lower competitive overlap between *Pithecia* and each of the other members of the Pithecinae, facilitating coexistence.

As primates increase in body size, metabolic costs per unit body weight become proportionally lower (Kleiber 1961), but absolutely more food is required (Bell 1971; Jarman 1974). Because larger body size confers greater energetic lability, however, larger species are more likely to show gut modifications and digestive strategies predicated on long retention time of food. The efficient digestion of plant cell wall material, particularly more lignified material, is a time-consuming process (Van Soest 1977, 1982). Van Soest (1982) has estimated that a body size of 10 kg or greater may be required for a digestive strategy predicated entirely on foregut fermentation. Most arboreal primates fall below this critical body mass, but because of lower energetic demands per unit body weight, larger primates should be able to exploit a wider range of fibrous materials more efficiently than smaller primates since they can "afford" somewhat slower food transit times.

Alouatta palliata is a moderate-sized arboreal primate (adult body mass 7–9 kg). As noted, members of this genus often live for long periods of time on diets consisting almost entirely of leaves, including some mature leaves. The relatively capacious hindgut and slow food passage rates provide conditions suitable for the efficient fermentation of plant cell wall material. Howler monkeys generally choose young leaves or mature leaves, which are unusually high in protein and relatively low in cell wall material (Milton 1979). Fermentation of such material should be more rapid than would be the case with most mature leaves (Van Soest 1977). Apparently because of limitations imposed by its body size and gut morphology, *Alouatta* must feed selectively, choosing leaves of high quality that provide maximal energetic and nutritional returns in exchange for the amount of time animals are able to invest in digesting them.

The three other moderate-sized primates examined in this study are all members of the subfamily Atelinae. *Ateles* falls in the middle of the three in body mass but has by far the most rapid turnover of ingesta. As noted, this genus is very strongly frugivorous. By passing a large volume of fruit through the gut each day and supplementing this basic fruit diet with selected leaf buds and young leaves, members of this genus are apparently able to satisfy all nutritional requirements. *Lagothrix* is somewhat smaller in body mass than *Ateles* and also has a somewhat slower food transit time. Field data show that animals eat fruits, leaves, and insects, probably more leaves and insects than is the case for *Ateles* (Izawa 1975; Kavanagh and Dresdale 1975). My data on captive animals suggest that *Lagothrix* may also be able to process harder fruits than *Ateles* (see appendix to this paper). *Lagothrix* occurs sympatrically with *Ateles*, but these data indicate that animals are feeding on somewhat different subsets of the available plant resources and that *Lagothrix* may also rely more heavily on foods from the second trophic level.

Brachyteles is the largest ateline and the largest neotropical primate. The adult female used in experiments weighed 12 kg (S. Rodriguez, personal communication), and free-ranging adults are reported to weigh some 15 kg (Aguirre 1971; J.C. Magalhães, personal communication). This large body size should confer sufficient energetic lability on animals so that they can exploit slower digesting foods efficiently. Data show that *Brachyteles* is highly folivorous (Milton, unpublished). In some months from 70% to more than 90% of total feeding time is spent eating leaves, including quantities of mature leaves. Animals also eat fruits and flowers when these are available but their dietary staple is foliage and animals are fully as folivorous as *Alouatta*. Like *Alouatta*, *Brachyteles* has a simple stomach and a capacious cecum and colon. Fecal material has the same curious pungent odor as that of *Alouatta*, and, similarly, shows a high content of endogenous fecal nitrogen (Milton, unpublished). These facts strongly suggest that *Brachyteles* routinely carries out fermentation of plant structural carbohydrates in the hindgut. The large body size of *Brachyteles* should enable it to be somewhat less selective than *Alouatta* when feeding. Faster food transit times with respect to TFA indicate that the digestive strategy of *Brachyteles* may be to take in copious quantities of leafy foods, holding such food in the gut only for sufficient time to extract the more accessible or degradable components, and then passing the more lignified material from the gut. In contrast, *Alouatta* is presumed to be a more selective feeder, taking in less lignified, higher quality leafy foods that can be more thoroughly degraded and then holding these foods in the gut for a longer fermentation treatment.

All of the Pongidae had approximately similar TFAs in spite of some considerable differences in adult body weight. Both chimps and orangs passed some 25% of the markers in the first 36–38 h after ingestion and 50%–67% within the first 48 h. My subjective impression was that chimps defecated smaller amounts more frequently than the orangs and had looser feces. Future trials may show that chimps pass more of a given meal within a 48-hour period than is the case for orangs. Field data indicate that chimps specialize more heavily on ripe fruits than is the case with orangs, who also eat quantities of unripe fruit as well as bark and leaves (Wrangham 1977; Rodman 1977, this volume). A strong dietary bias toward ripe fruit might well produce a pattern of frequent defecation of small amounts of fecal matter in chimps as is the case is *Ateles,* another ripe fruit specialist (Milton personal observation).

Adult gorillas appeared to retain a greater proportion of a given meal for a longer time than other pongids. They also show a somewhat greater relative volume in the colon than chimps and orangs (calculated from data in Chivers and Hladik 1980), and they are coprophagous (see also Harcourt and Stewart 1978). In the wild, gorillas eat both leaves and fruit, but leafy matter composes the greatest proportion of the diet; mountain gorillas may eat leafy material almost exclusively (Casimir 1975; Fossey and Harcourt 1977). The slow turnover time of meals and coprophagy strongly suggest that fermentation may provide gorillas with some of their required energy, and, by ingesting feces, they may also improve their protein and/or vitamin economies (McBee 1971).

The human subjects began to turn over food considerably more rapidly than either chimps or orangs, yet body weights were higher. The faster initial turnover rate in the human subjects may have been due to the more refined nature of their items of diet. Zoo-living pongids, however, are also eating somewhat refined diets. The slower TFA times of chimps and orangs could have been due to artificial feeding schedules characteristic of captive conditions. In general, however, it should be stressed than animal protein appears to be a more prominent dietary item for humans than for apes. Archaeological evidence indicates that hunting animal prey is in ancient trait in the hominid line (Isaac 1971). The small intestine of humans shows a greater relative volume than in apes, whereas apes show a greater relative volume in the area of the colon. Both the relatively large capacity of the human small intestine and the relatively rapid TFA times in my human subjects strongly support the inference that the human gut is particularly well adapted to process high quality dietary items that are volumetrically concentrated and rapidly digested. In a savanna-mosaic environment, higher quality dietary items are far more patchily distributed than in tropical forests (Milton 1981). In order to exploit such foods successfully, the ancestral line leading to modern hominids may have depended heavily both on meat protein in the diet and on overall increased food search efficiency to

afford the costs associated with a diet based on hyperdispersed, high quality foods (see Milton 1981). Mobility is presumed to be a critical feature in the exploitation of such a diet in a savanna-mosaic setting. Evidence from field behavior of gorillas, orangutans, and chimpanzees (see, for example, Rodman, this volume) strongly indicates that in the hominoid line, a high intake of bulky, fibrous or slowly digesting food stuffs results in decreasing mobility and a limited day range (gorilla and orangutan vs. chimpanzee). The heritage features of the hominoid gut appear to be such that decreasing dietary quality sets energetic limitations on an active lifestyle. Thus I would postulate that the ancestral line leading to modern humans was more chimp-like in its dietary habits than orangutan- or gorilla-like and that this same trend toward exploitation of high quality dietary items was retained and intensified during hominid evolution in a savanna-mosaic setting and is still characteristic of the hominid line today.

Overview

The data presented above are often scant and represent single trials, only for TFA's and often with only one subject. Before any firm conclusions can be drawn from these results, similar experiments should be repeated on a larger scale and in more depth. Nonetheless, these results do suggest a few tentative conclusions.

The feeding repertoire of any animal is a combination of its behavior, morphology, and physiology. But, depending on the animal examined and its dietary regime, one of these features may assume special importance in foraging success. Since most anthropoids are strongly dependent on plant foods, features of their internal morphology, particularly their gut morphology, might show specializations to help them overcome many of the chemical problems potentially inherent in plant-based diets. Data show that in some cases (i.e. howler monkeys, spider monkeys, and possibly *Pithecia*), the structure of the gut and its effect on food transit time plays a very important role in helping animals compensate for or overcome nutritional problems that would otherwise be posed by their choice of dietary items. A knowledge of food passage rates is therefore critical in helping us understand the food choice patterns in these species.

In other species, though gut morphology is obviously important, other features too assume considerable importance in the successful exploitation of a particular set of dietary items. For example, the specialized dentitions of *Chiropotes* and *Cacajao* help animals open the hard fruits and seeds constituting much of their diet; the manual dexterity of *cebus* aids in searching for insects among leaves and fronds, and facilitates the exploitation of hard foods. The enormous body size of the gorilla may be viewed as a special dietary adaptation because it provides the body mass apparently required for an animal in this lineage to exploit a diet consisting primarily of fibrous bulky foods that must be eaten in huge quantities and retained in the gut for considerable time.

Though there seems to be a general trend for smaller-bodied primates to turn over food more rapidly than larger-bodied primates, there are notable exceptions. *Pithecia* is a small primate that shows a very depressed food transit time, whereas *Ateles* is a much larger animal with an extremely accelerated food transit time. It should not be surprising that there are exceptions to the general broad relationships among body size, food choice, and food transit time. Obviously more research is necessary to elucidate the finer details of food processing in these and other species, but some knowledge of food passage rates is necessary first. Finally, I view competition for limited resources as the ultimate factor underlying these proximate mechanisms of gut morphology and digestive processes which, in effect, allow a particular primate species to use a subset of the available plant resources to a degree not presumed possible by other primate primary consumers in the habitat.

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Appendix

Other factors related to food processing efficiency can include the texture of foods eaten, mouth size and gape of the feeder, and features of the dentition. Below I present results of two experiments in which I investigated aspects of such influences on primate feeding patterns and food choice.

Feeding Rates in Howler Monkeys

Field data often show intraspecific as well as interspecific differences in food choice and feeding patterns. Such differences are typically attributed either to differences in body size or differences in the respective physiological states of given animals (Hladik 1977; Gaulin 1979). Though in many cases such explanations are doubtless correct, these differences also presumably reflect the fact that foods from different dietary categories are ingested at different rates and that intraspecific differences in body size exert an influence on the amount of food an animal can eat per unit time.

To determine the influence of food types and body size on feeding rates, three individually caged howlers (*Alouatta palliata*) were offered ad libitum access to a tared quantity of a particular food for a 5-minute period (table 9.2). After 5 minutes, the remaining food was removed and weighed to determine the amount ingested. This amount, when subtracted from the initial amount, gave the number of grams of food ingested per animal in the 5-minute trial period. This figure, divided by 5 gave the number of grams of food ingested per animal per minute.

Results of these trials, presented in table 9.2, show that adult howlers ingest ripe fig fruit approximately twice as rapidly as young leaves by weight. The juvenile howler ingested ripe fig fruit approximately three times as rapidly as young leaves. Thus, regardless of body size, ripe fruit of this type is eaten much more rapidly than young leaves. However, the number of grams of food ingested per minute appears to be a function of the body size of the feeder. The adult male weighed 56% more than the female and was able to eat young leaves 56% more rapidly and fruit 37% more rapidly. This male weighed 180% more than the juvenile and ate leaves 392% more rapidly and fruit 164% more rapidly. The same pattern was found when the adult female was compared to the juvenile. The female weighed 80% more than the juvenile and ate young leaves 176% more rapidly and fruit 93% more rapidly. These data suggest that for young howlers even a minor increase in body size can confer a considerable processing benefit in food intake by weight.

Table 9.2. Feeding Rates in *Alouatta palliata*[a]

Subject (Wt.)	Food	X̄ Grams Eaten Min^{-1} (fresh wt)	No. Trials
Adult male (8.4 kg)	*Cecropia insignis*, flush	19.8 ± 3.0	Five 5-min. trials
	Ficus insipida, flush	21.0 ± 5.8	Four 5-min. trials
	Ficus insipida, ripe fruit	37.0	One 5-min. trial
Adult female (5.4 kg)	*Cecropia insignis*, flush	12.9 ± 2.7	Four 5-min. trials
	Ficus insipida, flush	13.3 ± 1.0	Four 5-min. trials
	Ficus insipida, ripe fruit	27.0	One 5-min. trial
Juvenile female (3.0 kg)	*Cecropia insignis*, flush	4.8 ± 0.9	Four 5-min. trials
	Ficus insipida, flush	4.8 ± 1.0	Four 5-min. trials
	Ficus insipida, ripe fruit	14.0	One 5-min. trial

[a] One other adult female, weight 7.3 kg., in one trial with ripe *F. insipida* fruit ingested 26.9 g min^{-1} (one 5-min. trial).

Cecropia insignis flush: 74% water, total cell wall material (CWM) = 54.7% dry wt. of sample; *Ficus insipida* flush: 79% water, CWM = 37.5% dry wt.; *Ficus insipida* fruit: 78% water; CWM = 34.1% dry wt.

Hard Foods

In working on feeding ecology of howlers and spider monkeys in Panama, I noticed that both species avoided eating fruits protected by a hard exocarp and seeds protected by a hard endocarp (e.g., *Apieba membranacea* fruit, seeds of Palmae). The seeds of many such fruits are routinely eaten by other animals, which suggests that toxicity is not a factor here. This raised the question of whether howlers and spider monkeys avoided such foods because they did not choose to eat them or whether there was actually some more fundamental reason why such foods were avoided. To answer this question I offered commercial walnuts in the shell to the following caged primates: one *Alouatta palliata*, two *Ateles paniscus*, two *Lagothrix lagotricha*, one *Cebus albifrons*, one *Cebus apella*, and one *Cacajao melanocephalus*. The howler, spider monkeys, and uakari sniffed and/or bit and/or licked at the nut shell for a second or two, then dropped the nut and lost interest in it. Each woolly monkey immediately placed the nut in the canine area of the jaw, cracked it with no apparent effort and ate the nut. All three cebus monkeys reacted in precisely the same way to walnuts. They alternately bit at the shell and pounded the nut forcefully on various surfaces in the enclosure, apparently trying to chip or crack the shell. Once a crack appeared, the teeth were used to open the shell further so that the nut could be eaten.

These results suggest that both dental morphology and manual dexterity play a role in determining what members of a particular species will regard as potential food. Apparently animals lacking teeth suitable for crushing hard objects and/or lacking in manual dexterity to compensate for their relatively less powerful dentition or smaller gape do not perceive items such as walnuts as food. Other species immediately recognize these same items as highly desirable and edible and can circumvent the problems involved at getting at the edible portion. I believe that none of these animals had ever seen a commercial walnut before these feeding experiments (although all may have seen nuts in the wild before capture), and so all were presumably equally naïve with respect to that potential food. These tests should be repeated with more animals and a greater variety of hard foods. The one *uakari* used in the experiments was a very small female, and I regard results with this animal as inconclusive.

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