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FOOD CHOICE AND DIGESTIVE STRATEGIES OF TWO SYMPATRIC PRIMATE SPECIES

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The ecological literature on food choice in animals has focused primarily on external rather than internal features. Food choice has been correlated with such features as body size (Hespenheide 1971, 1975; Ricklefs 1972; Diamond 1975), bill size (Schoener 1965), and head or jaw length (Schoener 1967; Werner 1977). In some cases, however, the most critical determinants of food choice may be internal and hence not readily detected. In this paper I analyze the digestive morphology of two sympatric primate species, both primary consumers, and suggest that resource specialization is related to gut size and food passage rates.

DIGESTIVE STRATEGIES

The digestion of food represents a compromise between two conflicting forces: efficiency of nutrient extraction and food passage rate (Van Soest 1981). Retention of food in the digestive tract for long periods of time maximizes extraction of nutrients from each meal, but reduces the amount of food the animal can process per unit time. Conversely, rapid passage of food through the digestive tract reduces the efficiency of nutrient extraction, but increases the amount of food that can be processed. In effect, there is an "efficiency-velocity" continuum and animals can be ranked along this continuum depending on whether they tend to maximize food value per given meal or maximize the volume of food processed per unit time.

Bell (1971) stressed this point in his discussion of the digestive strategies of plains-living African ungulates. Some ungulates (e.g., buffalo) are characterized by elaborate foregut specializations (sacculated stomach). These species are more efficient at extracting nutrients from a given meal than similar-sized herbivores that lack such specializations. However, they have slower rates of food passage, and since each meal therefore represents a greater time commitment, they tend to be more selective feeders to avoid loading the digestive tract with relatively low quality foods.

Other ungulates (e.g., zebra), which lack comparable foregut specializations, are less efficient at extracting nutrients. However, they have faster rates of

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passage and since they can therefore process more food per unit time, they tend to be less selective feeders. In other words, they can make up for their lower margins with higher volume. Further advantages and disadvantages of these two basic digestive strategies are discussed in Bell (1971) and more recently in Janis (1976) and Uden (1978).

Bell's study makes it clear that without some knowledge of an animal's digestive strategy, its choice of food may be difficult to explain. Without such information there is no means of determining what mechanisms may limit food choice and thus perhaps ameliorate potential competition between sympatric species with similar diets.

Here I relate food choice to relevant morphological features in two primate species, *Alouatta palliata* (mantled howler monkey) and *Ateles geoffroyi* (black-handed spider monkey), living sympatrically in the lowland tropical forest on Barro Colorado Island, Panama. Past studies of feeding behavior of these two species are summarized in table 1 and show that howler monkeys depend heavily on leaves in the diet while spider monkeys depend heavily on fruit. As a general rule, howlers eat both leaves and fruit each day (Milton 1978, 1980). At times of year when fruit is in short supply, however, particularly during the transition period between the wet and dry season (November–December), howlers shift to a diet consisting almost entirely (85% of daily feeding time) of leaves. Similar high percentages of leaf eating have been reported for howlers living in riparian forests of Costa Rica (i.e., > 90% of daily feeding time; Glander 1975). At other times of year, when fruit is more abundant, howlers may spend 50% or more of daily feeding time eating fruit; regardless of how much fruit is available in the forest, howlers invariably eat some leaves each day (Glander 1975; Milton 1978, 1980).

Spider monkeys, on the other hand, are extremely frugivorous. Over an annual cycle on Barro Colorado, 72% of daily feeding time was spent eating fruit and 80% wet weight of the annual diet of spider monkeys is believed to come from fruit pulp (Hladik and Hladik 1969). In Colombia, over an annual cycle, spider monkeys spent an estimated 83% of total feeding time eating fruit and only 7% eating leaves (Klein and Klein 1977). During the transition season on Barro Colorado, as noted above, a time of low fruit availability, spider monkeys still spent a daily average of 60% of feeding time eating fruit by exploiting all apparent fruit sources in the habitat (table 1).

Ripe fruit pulp of the type eaten by spider monkeys is generally quite low in protein (table 2). This raises the question of where spider monkeys may be obtaining their required protein each day. On the other hand, at times howlers eat large quantities of leaves which are very low in nonstructural carbohydrates. How then do howlers meet their energy requirements when living on high foliage diets? Further, when fruit is in short supply, why don't spider monkeys switch to leaves as a principal food source? Why do howlers eat leaves each day even though at times there is a demonstrated hyperabundance of fruit? To see how these questions, which involve food choice, might be related to the digestive strategies of howlers and spider monkeys, I carried out feeding trials on both species to obtain estimates of food passage rates.

TABLE 1

COMPARATIVE DATA ON HOWLER AND SPIDER MONKEYS, BARRO COLORADO ISLAND, PANAMA

	APPROXIMATE LENGTHS AND WIDTHS, SECTIONS OF DIGESTIVE TRACT (cm)					PRINCIPAL DAILY ACTIVITY PATTERNS (%) AND $\bar{X}$ DAY RANGE*		
SPECIES	Stomach	Small Intestine	Caecum	Colon	DIET, % FEEDING TIME	Rest	Travel	Feed
		Length						
Alouatta palliata ..... (adult wt, 7–9 kg)	21	126	18	43	Annual cycle: 48% leaves, 42% fruit, 10% flowers	65.5 ± 6.98	10.2 ± 3.6	16.2 ± 4.3
		Width						
	9	2	6.5	3.5	Transition season: 85% leaves, 10% fruit, 5% flowers	$\bar{X}$ Day range = 443 ± 148 m		
		Length						
Ateles geoffroyi ...... (adult wt, 7–9 kg)	15	90–120†	22	33	Annual cycle: 72% fruit, 22% leaves, 6% flowers	53.7 ± 9.45	16.4 ± 6.59	25.7 ± 7.12
		Width						
	9	1.5	6.5	1.5	Transition season: 60% fruit, 37% leaves, 3% flowers	$\bar{X}$ Day range = 915 ± 348 m		
					Annual cycle: *A. belzebuth*, Colombia: 83% fruit, 7% leaves and buds, 10% other (Klein and Klein 1977)			

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[*] Daily activity patterns and day range derived from 9 mo of systematic data collection on *Alouatta palliata* (Milton 1977) and 8 mo on *Ateles geoffroyi*. In both cases, samples covered portions of dry, wet, and transition seasons on Barro Colorado.

[†] It was extremely difficult to accurately measure the small intestine; this may be considered a best estimate.

TABLE 2

ESTIMATES OF PROTEIN AND TOTAL NONSTRUCTURAL CARBOHYDRATES IN SOME FOODS OF HOWLERS AND SPIDER MONKEYS (% dry wt.)

Plant Species	Part Eaten	% Protein* (total $N \times 6.25$)	% Total Nonstructural Carbohydrates† (TNC)
Paullinia bracteosa	Young leaf, open	21.44	1.1
Inga goldmanii	Young leaf, open	21.94	.5
Ceiba pentandra	Young leaf, open	22.31	.1
Dipteryx panamensis	Young leaf, shoot	23.56	2.4
Ficus yoponensis	Young leaf, rolled	11.56	4.0
		$\bar{X}$ = 20.16 ± 4.87	$\bar{X}$ = 1.62 ± 1.59
Tetragastris panamensis ..	Ripe fruit, pulp	3.25	56.3
Doliocarpus major	Ripe fruit, pulp	4.50	21.1
Spondias mombin	Ripe fruit, pulp	4.30	40.0
Quararibea asterolepis	Ripe fruit, pulp	5.44	31.0
Spondias radlkoferi	Ripe fruit, pulp	11.69	24.6
		$\bar{X}$ = 5.84 ± 3.36	$\bar{X}$ = 34.6 ± 14.10

NOTE.—See Nagy and Milton (1979*b*) for food consumption rates for *Alouatta palliata*. An examination of the intestinal tract of a fresh *A. palliata* cadaver (adult male) gave a wet weight of ca 650 g for stomach plus all contents. The stomach appeared packed to capacity with fig fruit mash and the animal had recently finished feeding. An adult male *Ateles geoffroyi* was offered 700 g wet weight of fig fruit mixed with a small amount of bread and all bran. Some 590 g of this mixture were eaten; however, the stomach of this animal may have been partially filled prior to this feeding. There are no estimates for wet weight fills for other sections of the digestive tract of either species.

* Protein values were obtained using a Technicon BD-40 digestor to estimate total nitrogen and multiplying these results by 6.25. This probably overestimates available protein due to nonproteinaceous N present in the samples.

† Total nonstructural carbohydrates were obtained by the modified Weinmann method. See Milton (1979) for further details of this technique and additional data on chemical components of plant samples from the Barro Colorado forest.

MATERIALS AND METHODS

Four howler monkeys (*Alouatta palliata*) and eight spider monkeys (7 *Ateles geoffroyi*, 1 *Ateles paniscus*) were used in the feeding trials. Animals were housed in metal cages under open air conditions. As shown in table 3, study subjects were of different ages and sexes. One howler had been raised in captivity from infancy; the other three were wild animals captured for the experiments with tranquilizing darts. All spider monkeys but one had been born in captivity or maintained in captivity for at least 2 yr prior to the experiments. The eighth spider monkey, a wild male, was baited into an outdoor enclosure with food and then held for the experiments.

To obtain estimates of food passage rates, small colored plastic strips were concealed in foods and fed to the animals at timed intervals. Wild howlers were fed natural items of diet collected from the nearby forest. These included fruits of *Ficus insipida* and *F. yoponensis* and leaves of *F. insipida* and *Cecropia insignis*. The fourth howler and one juvenile spider monkey were fed identical diets consisting of lettuce, fresh fruit (bananas, apples, and oranges), cottage cheese, and

TABLE 3

TIME OF FIRST APPEARANCE OF MARKERS IN HOWLER AND SPIDER MONKEYS

Species	Date and Time of Feeding of Markers	First Appearance of Markers (h)
Alouatta palliata palliata		
captive ♂	May 3, 1978 0900	22.5
	May 4, 1978 0800	23.5
	May 5, 1978 0830	23
	Nov. 9, 1978 1415	16.75
wild ♂	Feb. 5, 1978 0930	23.75
	Feb. 7, 1978 1630	16.25
wild ♀	Feb. 5, 1978 0930	23.5
	Feb. 7, 1978 1630	16.25
wild, juv. ♀	Feb. 5, 1978 0930	22.25
	Feb. 7, 1978 1630	16.25
		$\bar{X}$ Passage time = 20.4 ± 3.50 h
Ateles geoffroyi panamensis		
captive ♀	May 11, 1978 0800	5.25
captive ♀	May 11, 1978 0800	3.25
captive, juv. ♀	May 3, 1978 0900	3
	May 4, 1978 0800	5.75
	May 5, 1978 0830	4.5
	May 7, 1978 0815	3.75
captive, juv. ♀	May 11, 1978 0800	5.25
wild ♂	Nov. 9, 1978 1415	2.75
Ateles geoffroyi yucatanensis		
captive ♀	May 11, 1978 0800	5.25
captive ♀	May 11, 1978 0800	7.75
Ateles paniscus paniscus		
captive ♂	May 10, 1978 1345	2.75
	May 11, 1978 0800	3.25
		$\bar{X}$ Passage time = 4.38 ± 1.53 h

NOTE.—Feeding trials recently carried out on one *Alouatta fusca* (Jardim Zoological do São Paulo) and four *Ateles paniscus* (CAP Jardim Zoological do Manaus) gave results very similar to those cited above.

several slices of bread. Six spider monkeys were fed diets consisting of bananas, cottage cheese, and several slices of bread. The wild spider monkey was fed fruit of *F. insipida* mixed with bananas and several slices of bread.

RESULTS

Colored markers fed to howlers between 0800–0930 of one day began appearing in the feces between 0700–0800 the following day (table 3). Markers fed to howlers at 1630 of one day first appeared in the feces between 0700–0800 the following day. Thus transit time of markers with respect to first appearance averaged 20.4 ± 3.50 h; some 23 h if fed in the A.M. and some 16 h if fed in the P.M. Based on estimates of the number of colored markers in each set of feces, howlers appear to pass the bulk of a given meal within 30 h after the initial feeding.

Colored markers fed to spider monkeys at 0800 of one day began appearing in the feces around 1100–1300 that same day (table 3). Markers fed to spider monkeys around 1400 of one day began appearing in the feces around 1700 that same day. Time of first appearance in spider monkeys thus averaged 4.4 ± 1.53 h, with a range of 2.75 to 7.75 h. Based on estimates of the number of colored markers in each set of feces, spider monkeys appeared to pass the bulk of a given meal within 8 h after the initial feeding.

No howler monkey began to pass markers on the same day in which it was fed. All spider monkeys began to pass markers on the same day in which they were fed. Time of first appearance for howlers (n = 10) and spider monkeys (n = 12) differ significantly (two-tailed Mann-Whitney U test, $P < .002$).

Since both monkey species were fed similar diets and indeed, at times, identical diets, these interspecific differences in food passage rates cannot be due to variations in the passage rates of particular types of food. Further, howler monkeys showed the same passage rates whether they were eating diets high in fig fruits or high in fig leaves.

Both species showed differential rates of passage. Markers fed to animals in one day generally continued to appear in the feces, at least in small amounts for a minimum of 24 h after the initial feeding. In one case, three different sets of colored markers were found in the feces of one howler which indicates that some food particles may be retained in the howler digestive tract for as long as 72 h. Most markers fed to spider monkeys tended to be excreted within some 4–8 h after the initial feeding but the continued appearance of at least a few colored markers 24 h after the initial feeding indicates that some food is retained in the digestive tract for a longer period of time. Attempts to get animals to eat chromium-bonded alfalfa so that digestion curves could be constructed were unsuccessful as both species refused to eat this material.

Measurements of sections of the digestive tract of two monkeys, one an adult male howler and the other an adult male spider monkey, were taken to determine relative gut capacities of each species. As shown in table 1, the length and width of the stomach, small intestine, and caecum of both species were roughly equivalent. The colon of the howler, however, was some 43 cm long with a width of 3.5 cm as contrasted with that of the spider monkey which measured only around 33 cm by 1.5 cm. Work by Hladik (1967) on the relative surface area of sections of the digestive tract in 24 primate species [relative surface area = actual surface area/(length of body + head)^2 × 1,000] also showed that howlers and spider monkeys differed little in the amount of relative surface area of the stomach (50 for howlers vs. 60 for spider monkeys), small intestine (300 vs. 280), and caecum (40 vs. 35), but they differed considerably at the level of the colon (160 vs. 80; Hladik 1967).

It thus appears that gut capacities for the two species (which have approximately equal adult body weights) are roughly equivalent until the area of the colon, where howlers have a decidedly greater capacity. Ingesta are apparently retained in the capacious colon for some time after passage out of the caecum. In spider monkeys, however, ingesta should be very rapidly excreted after they have passed out of the caecum. The much faster food passage rate of spider monkeys indicates that they can process considerably more food per unit time than howlers.

In fact, spider monkeys spend a greater percentage of their daily time feeding than howlers (table 1) and are eating considerably more fruit, which can generally be eaten about twice as fast as young leaves g^{-1} min^{-1} wet weight (Nagy and Milton 1979*b*).

DISCUSSION

With their extensive hindgut area and slow food passage rates, howler monkeys appear committed to a strategy of efficient digestion, which enables them to live on diets high in foliage when fruits and flowers are in short supply. When fruit is readily obtained, they eat it, but they always eat some leaves. Since the type of fruit howlers eat is generally low in protein and the morphology of the howler gut permits only a slow rate of passage of food particles (i.e., 16–24 h for first appearance, 30+ h to pass the bulk of a given meal through the tract), they probably could not process a sufficient volume of fruit each day to meet their protein requirements. So they must eat some leaves. And since each meal represents a great time commitment (in processing), they must be highly selective in feeding; i.e., they must choose leaves of a high nutritional quality to meet their dietary requirements (Milton 1979, 1980; Nagy and Milton 1979*a*).

When fruit is scarce, howlers increase the amount of time spent feeding on leaves. Since they are less active than spider monkeys, they require fewer kcal per day. Further, since their hindgut is more capacious, there is more scope for fermentation activities. It is estimated that howlers may obtain between 26% and 36% of required daily energy from fermentation end products (volatile fatty acids) depending on the types and amounts of foods eaten (Milton et al. 1979; Milton et al. 1980). These energy-rich fermentation end products should be particularly valuable to howlers when they are living on diets high in foliage.

Conversely, spider monkeys appear committed to a strategy of rapid food passage. They eat primarily fruit, which is generally rich in nonstructural carbohydrates but low in protein. However, like some ungulates described by Bell (1971), they evidently can process a considerable volume of food per unit time. By passing quantities of fruit rapidly through the digestive tract each day (i.e., 4.4 h average time of first appearance, 8+ h to pass the bulk of a given meal through the tract), and supplementing this basic fruit diet with some young leaves and leaf buds, spider monkeys should be able to meet demands for both energy and protein.

Spider monkeys, like howlers, showed differential rates of passage of colored markers. This suggests that some food particles take longer to pass through the digestive tract than others. It is probable that some fermentation activity, particularly fermentation of fruit pectins, also takes place in the caecum of spider monkeys. End products of fermentation may therefore provide them with some energy and possibly some amino acids or trace nutrients (Hungate 1967). However, since spider monkeys lack the hindgut volume and slow passage rates that are essential for the efficient fermentation of fibrous plant parts (Bauchop 1978; Parra 1978), they presumably derive a far lower return from such processes than howlers.

In effect, each of these primate species is living on a diet that is not tenable for the other. On a diet composed of fruit of the quality presented in table 2, howlers with their slow food passage rates would not be able to meet protein requirements. On a primarily leaf diet, of the quality presented in table 2, spider monkeys would not be able to meet demands for energy. Once a particular digestive strategy has evolved, with its attendant morphological, physiological, and behavioral adaptations, diet switching, at least over the short run in evolutionary time, does not seem possible. Animals with voluminous sacculated guts cannot suddenly adopt dietary strategies predicated on fast rates of passage, while animals with short narrow guts cannot suddenly become efficient fermenters of plant fiber. Animals can alter their feeding rates as well as the amount of food eaten per unit time, at least up to a point (Slansky and Feeny 1977). However, in general, since food passage rates are so intimately bound up with gut morphology, unless there are special structures in the digestive tract to permit unusual lability, species committed to efficiency must continue to digest accordingly, as must those species committed to fast rates of passage, regardless of how the resource base alters over the short run. Thus each species can utilize a subset of the available resource base to a degree that the other cannot; in this sense, such specializations can be said to confer a selective advantage. It is suggested that competition for dietary resources may have been an ultimate factor in producing these proximate mechanisms.

SUMMARY

Critical determinants of dietary choice in animals may be internal rather than external and hence not readily detected by field observation. Digestive strategies of two sympatric primate species, howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), both primary consumers, were investigated by carrying out feeding trials to determine food passage rates and by examining selected aspects of gut morphology.

On the average, a given marker took 20.4 ± 3.5 h to first appear in the feces of howler monkeys as contrasted with a mean of 4.4 ± 1.5 h for spider monkeys. Gut morphology showed that howlers had colons approximately double the size of those of spider monkeys.

Howler monkeys are highly folivorous while spider monkeys are primarily frugivorous. Yet leaves are generally low in nonstructural carbohydrates while fruits are low in protein. Howlers, with their capacious hindguts and slow food passage rates, are able to ferment refractory plant parts more efficiently than spider monkeys and in this way can maximize energy returns from leaves. Conversely, spider monkeys, with smaller hindguts than howlers, are able to process greater quantities of food per unit time. In this way they can specialize on fruits, which are generally too low in protein to support howlers.

Once a particular digestive strategy has evolved, with its attendant morphological, physiological, and behavioral adaptations, diet switching, at least over the short run, does not appear possible.

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