





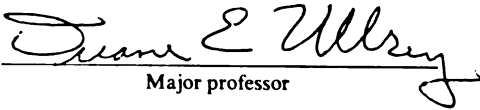
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**COMPARATIVE ADAPTATIONS TO FOLIVORY
IN PRIMATES**

presented by

Mark Stephen Edwards

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Animal Science


Major professor

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ABSTRACT

COMPARATIVE ADAPTATIONS TO FOLIVORY
IN PRIMATES

By

Mark Stephen Edwards

COMPARATIVE ADAPTATIONS TO FOLIVORY
IN PRIMATES

Volume I

This study is divided into two major sections. The first examines feeding habits and nutrient composition of natural diets of free-ranging red howlers (*Alouatta seniculus*). The second focuses on digestive capabilities of several captive primate species.

By

Mark Stephen Edwards

Daily activities and number of bites of food were recorded during monthly observations of a group of 12 free-ranging red howlers. The group was transferred to a new facility. These animals were used in a study of the effect of an artificial bite foraging device on feeding behavior of 12 animals.

A DISSERTATION

Submitted to
Michigan State University
for partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Feeding on 85 plant species and parts, including leaves (82.0%), fruits (31.2%), flowers (13.1%), and other parts were analyzed for proximate, fiber, and mineral composition. Combining observations of bite counts, bite weights, and

1995

ABSTRACT

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By

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This study is divided into two major sections. The first examines feeding habits and nutrient composition of natural diets of free-ranging red howlers (*Alouatta seniculus*). The second focuses on digestive capabilities of several captive primate species.

Daily activity, feeding behavior, food items selected, and number of bites of food were recorded during monthly observations over a 12-month period of two groups of free-ranging red howlers. After 5 months of observation, one group was transferred to an on-site holding facility. These animals were used as models to determine weights of an individual bite for specific plant parts consumed by adult animals (1♂, 2♀♀). Representative plant samples were collected monthly for nutrient analyses. Daily activities included resting (75.4%), feeding (12.6%), moving (7.5%), and other behaviors (4.0%). Feeding time was distributed over 85 plant species and parts, including leaves (52.9%), fruits (31.2%), flowers (13.1%), and other items (2.8%). Ninety-one plant parts were analyzed for proximate, fiber, and mineral composition. Combining observations of bite counts, bite weights, and

nutrient analyses, a nutrient profile of the natural diet was developed. Daily fresh weight and dry matter intake were estimated to be 544.0 g and 151.0 g, respectively. Daily gross energy intake was estimated to be 711.2 kcal. Nutrient concentrations in diet dry matter were estimated to be 13.4% crude protein, 51.5 % NDF, 37.8% ADF, and 19.0% cellulose.

Based upon estimated fiber concentrations in the wild diet, a higher fiber primate diet was developed for captive feeding trials. Two test diets with different levels of fiber (15% ADF, 30% ADF) were fed to primates with simple gastrointestinal tracts (ruffed lemurs), hindgut fermentation (howlers), and foregut fermentation (colobines). Apparent digestibility (%) of dry matter (DM), gross energy (GE), and fiber components (NDF, ADF, C, HC) were measured in the three gut types. Rates of digesta transit (TT_1) and retention times (R_{gut}) were assessed using acetate beads, Co-EDTA, and Cr-mordanted fiber. Animals with simple gastrointestinal tracts had lowest digestibilities (%) of DM (51.0, 41.7), GE (47.0, 39.7), and NDF (20.4, 20.7) for 15ADF and 30ADF, respectively. Hindgut fermenters exhibited greater digestive capabilities for (%) DM (69.3, 61.7), GE (68.5, 61.5), and NDF (44.8, 47.4) for 15ADF and 30ADF, respectively. Colobine primates were most efficient in digesting (%) DM (81.2, 76.6), GE (80.9, 75.6), and NDF (77.1, 74.7) in 15ADF and 30ADF, respectively. TT_1 was fastest in simple gut species and slowest in foregut fermenters. R_{gut} was shortest in simple gut species and

longest in foregut fermenters. No significant differences between marker types were detected. Development of a higher fiber (>25% ADF) primate diet is warranted based upon these results.

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DEDICATION

This dissertation is dedicated to my parents, William Patrick and Suzanne Edwards, and my wife, Michelle. Their unwavering support and love have been a constant throughout my life and have greatly influenced my work.

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ACKNOWLEDGEMENTS

As with any project of this magnitude, the number of people who helped toward the completion of this work, to which I owe a great deal, is great. My appreciative thanks go out to my graduate committee for their support and guidance throughout the duration of my program. Dr. Deane S. Ulrey, my major advisor, has provided criticism, encouragement,

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This dissertation is dedicated to my parents, William Patrick and Suzanne Edwards, and my wife, Michelle. Their unwavering support, love, and sacrifice throughout my life have created endless opportunities for me.

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Plant Material as a Food Source

Structural polymers are the most abundant source of energy in plants (Parra, 1978). ...

Chapter I

Nutritional Strategies of Herbivores

Introduction

The co-evolution of plants and the animals that eat them has led to adaptations of both the consumers and the plants. Mammals that consume plant materials rich in structural carbohydrates are commonly referred to as herbivores. Eisenberg (1978) distinguished between species that consume grasses and forbs with little or no woody tissue, which were termed herbivores, and species that specialize on a diet of arboreal leaves, which he termed folivores. The ability of animals to use the structural carbohydrates in plants as food is dependent upon the capacity of gastrointestinal microbes to degrade them and of the ability of the host to use the end-products of microbial fermentation and the microorganisms themselves (Van Soest, 1982).

Plant Material as a Food Source

Structural polymers are the most abundant sources of energy in plants (Parra, 1978). However, vegetative plant

parts are relatively low in digestible nutrient concentrations (Langer, 1988). The structural carbohydrates which make up plant cell walls, include cellulose, hemicelluloses, and related compounds (lignins) that are resistant to digestion by mammalian enzymes. Availability of the energy within these compounds depends on an ability to cleave glycosidic bonds within plant carbohydrates and between plant carbohydrates and other substances (Van Soest, 1982). Mammalian digestive enzymes can hydrolyze α 1-4 and α 1-6 glycosidic linkages in starches and sugars. However, enzymes required to hydrolyze the β 1-4 glycosidic linkages between individual glucose units of cellulose and hemicellulose are lacking in the digestive secretions of almost all animals (Moir, 1968; Van Soest, 1977).

Cellulose is the most abundant carbohydrate in the world, but is not found independently in plant cell walls. Rather, it is combined with lignins, hemicellulose, cutin, and minerals. The availability of cellulose as a source of energy for herbivores varies from total digestibility to complete indigestibility, depending upon the extent of lignification and the presence of other interfering compounds (Van Soest, 1982). Studies of the relationship of cellulose to lignin have produced alternative views concerning the nutritive value of cellulose. One view suggests that the nutritive value of cellulose is regulated by its ratio with lignin. An opposing

view is that there are two types of cellulose, one of which is lignified and resistant to digestion and another that is free of the protective properties of lignin (Van Soest, 1982).

Hemicellulose is a highly complex mixture of polysaccharides with β 1-4 linkages in the main xylan core polymer. Hemicellulose is more closely associated with the lignin fraction of the plant cell wall than other polysaccharides (Sullivan, 1966). Like cellulose, the digestibility of hemicellulose is negatively correlated with the extent of lignification. However, the digestion of hemicellulose by ruminants is not accomplished in the same manner as is digestion of cellulose. Nonruminant herbivores typically digest relatively more hemicellulose than cellulose, whereas ruminants usually digest approximately equal quantities of both carbohydrates (Van Soest, 1994).

After cellulose, lignin is the most abundant of all natural polymers (Nimz, 1974) and is comprised of high molecular weight phenylpropanoid units. Lignin is not a single substance but a collection of monomeric units of different dimensions. As a result, the characteristics of lignin fractions are variable among plant species and among plants at different stages of maturity. Grass lignins are considerably more soluble in alkali than are lignins from either woody plants or forage legumes (Van Soest and Wine, 1967). The structural rigidity that lignins provide to plants

may be one of their most important benefits, but their presence tends to lower the value of plants as food.

The degradation of lignin is dependent upon oxidation and is resistant to anaerobic microbial fermentation in the gastrointestinal tract. As a consequence, lignin is a very important factor in reducing the digestibility of plant fiber by herbivores (Van Soest, 1967; Deinum, 1971; Parra et al., 1972). The precise manner in which lignin limits digestibility is the subject of numerous theories and is poorly understood.

Crude lignin is the collective analytical term for the noncarbohydrate fraction of plants that is resistant to enzymatic and acidic hydrolysis. There is no routine analytical procedure that will determine true lignin (Van Soest, 1982).

Other components of the plant cell wall include pectins, xylans, and gums. Pectin is a polysaccharide, high in galacturonic acid content, which has cementing properties. Although included with other soluble fractions in the measure of dietary fiber used in human nutrition, pectin is dissolved by neutral detergent (ND) and thus is not included with other plant cell wall components in the neutral detergent fiber (NDF) fraction or residue.

Cutin is a structural, aliphatic polymer component of the plant cuticle. Suberin, a mixed aromatic-aliphatic polymer,

is found between the plant cell wall and cytoplasm. The cell walls of browse plants may contain up to 15% of a cutin-suberin complex (Robbins and Moen, 1975). Although these two compounds are partially digestible (Brown and Kolattukudy, 1978), they may reduce the digestibility of more readily available cell wall polysaccharides through physical obstruction.

Secondary plant metabolites comprise a broad group of compounds which exhibit a range of characteristics from bitter taste to toxicity. They include, but are not limited to, tannins, flavonoids, terpenes and essential oils, alkaloids, and coumarins. Few of these compounds have any primary metabolic functions within the plant, hence their classification as "secondary compounds".

Tannins are low molecular weight, polymerized, soluble phenolic compounds. Although tannins are only one of many groups of compounds that are responsible for feeding aversion to plants, they appear to be the most important (Swain, 1978). Four groups of tannins are defined based upon chemical structure, molecular weight, water solubility, and tannin action: hydrolyzable and condensed tannins (proanthocyanidins), oxytannins, and a group of miscellaneous tannins referred to as β -tannins (Swain, 1977; Swain, 1978). Tannins are capable of binding almost all soluble proteins and macromolecules such as nucleic acids and polysaccharides. The

result is the precipitation of cellular proteins and dramatic reductions in digestive enzyme activity, sometimes to zero (Rhoades and Cates, 1976; Lohan et al., 1981). Tannins found in browse plants consumed by ruminants may also inhibit cellulase activity of microbes (Mandels and Reese, 1963; Robbins et al., 1975). Humans (Harborne, 1979).

Evidence supporting the role of tannins as a defensive mechanism of plants against herbivory has been explored (Levin, 1971; Levin, 1976; Harbourne, 1977; Swain, 1977). Feeding studies, including those with *Colobus* spp. (Oates et al., 1977) and *Gorilla* spp. (Harbourne, 1977), suggest that tannin concentrations greater than 2% may deter feeding.

The terpenoid class represents one of the largest and biologically most important classes of natural products (Mabry and Gill, 1979), which include steroids and saponins. Saponins are a widespread group of secondary plant metabolites characterized by their "soaplike", foam-forming properties. This action of saponins has been suggested to contribute to ruminant bloat. Saponins may alter the surface tension of the ruminal contents, leading to entrapment of gaseous microbial end-products as a froth (McCandlish, 1937; Quin, 1943; Applebaum and Birk, 1979). Nonruminant species exhibit different responses to saponins, with food aversion as a primary response, associated with their bitter taste (Cheeke, 1976). The effect and the chemical composition of foods

A group of aromatic secondary plant metabolites known as flavonoid pigments, contribute to the color of plants. The toxicity of common flavonoids to insects has been established with studies of the tobacco bud worm (*Heliothis virescens*) (Shaver and Lukefahr, 1969). However, common flavonoids are apparently harmless to humans (Harborne, 1979).

The alkaloids are structurally a very diverse group of compounds (Robinson, 1979) that can exhibit pharmacological activity and inhibit digestion.

Mammalian Adaptations to Herbivory

Mammalian herbivores have developed a wide variety of physical adaptations which promote, either through symbiotic microbial fermentation or mechanical action, the destruction of the structural and chemical defenses of the plants upon which they feed. Van Soest (1982) classified several herbivorous mammals based upon their gastrointestinal anatomy (Table 1-1).

The presence of bacteria, and frequently protozoa, in the digestive tract of most animals is common. Plants which contain a high concentration of structural carbohydrates can be digested with the assistance of these microorganisms. The benefit of these organisms to the host animal, and the end-products produced, is directly related to the structure of the digestive tract and the chemical composition of foods

Table 1-1. Classification of some mammals based on gastrointestinal tract anatomy (Van Soest, 1982).

Class	Species	Dietary habit
Pregastric fermenters		
Ruminants	Cattle, sheep	Grazing herbivore
	Deer, antelope	Selective herbivore
Nonruminant	Colobine monkey,	Selective herbivore
	hamster, vole	
	Kangaroo, hippopotamus	Grazing and selective herbivore
Hindgut fermenters		
Cecal (rodents)	Capybara	Grazer
	Rabbit	Selective herbivore
	Rat	Omnivore
Colonic digester		
Sacculated	Horse	Grazer
	New World monkey	Selective herbivore
	Pig, human	Omnivore
Unsacculated	Dog	Carnivore
	Cat	Carnivore

consumed. The size of lignified plant tissues, creating

Two principle gastrointestinal tract types that support herbivory involve enlargements of the stomach or the hindgut to accommodate microbial fermentation (Parra, 1978; Langer, 1988). A third type of gastrointestinal tract seen in a few herbivores (e.g., pandas) involves no enlargements or sacculations (Dierenfeld et al., 1982; Warnell, 1988; Warnell et al, 1988). occupy enlarged areas distal to the gastric.

Ruminants and other foregut fermenters have a large sacculated foregut that is the primary site of microbial activity. Within the foregut are anaerobic cellulolytic bacteria, and other microbial symbionts, which produce enzymes that degrade plant cell walls and promote access to cellular contents. The foregut fermenter class of gastrointestinal tracts permits microbial fermentation to precede gastric and enzymatic digestion. Moir (1968) listed a number of animals which possess a sacculated foregut-type digestive tract including macropod marsupials, some edentates, hippopotami, camels, and colobine monkeys. These species exhibit evolutionary convergence with ruminants in their adaptations of foregut structure for folivory (Moir, 1968). have developed

The process of rumination (regurgitation and re-mastication of digesta) is an important mechanism that assists in reducing the protection afforded cell contents by lignin. The additional physical processing by rumination helps reduce

the particle size of lignified plant tissues, creating "openings" that permit access for microbial symbionts. However, not all species that have adaptations for foregut fermentation ruminate. Thus, the type of plant fiber and extent of lignification may have different effects on these species than on ruminants. The VFAs produced, acetic, butyric. In animals with hindgut fermentation, symbiotic microorganisms occupy enlarged areas distal to the gastric. These animals are unable to recover quantitatively as high a proportion of the nutrients produced by fermentation as are foregut fermenters. This decreased return on microbial fermentation may be due, in part, to a faster rate of digesta passage through the lower gut, thus limiting the time available for absorption.

Herbivorous species that lack apparent gastrointestinal adaptations for fermentation present a paradox to nutritionists and physiologists. The contribution of plant material to the diet of these species varies from only a fraction to 100%. However, the extent to which these species benefit from fermentation by microbial symbionts is limited. These species (e.g., red pandas, giant pandas) have developed other strategies to exist on a relatively indigestible diet. These include increased rates of digesta transit and short retention time allowing consumption of relatively large daily amounts of food of low nutrient value (Warnell, 1988; Warnell

et al., 1989). Anaerobic fermentation of plant material by gastrointestinal microorganisms converts substrate into microbial cells and fermentation end-products. The end-products of fermentation include volatile fatty acids (VFAs), carbon dioxide, and methane. The VFAs produced, acetic, butyric, and propionic, can be important sources of energy for the host. The microbial cells can be important sources of B-complex vitamins, amino acids, and vitamin K.

As indicated above, adaptations to feeding on plant material demonstrated by mammals are not limited strictly to gastrointestinal tract modifications. The chemical composition of plant tissues varies greatly among different plant parts and among stages of plant maturity. This is true with respect to both structural carbohydrates, lignin, and some secondary plant metabolites. For example, mature oak leaves have a higher concentration of tannins than immature oak leaves (Feeny, 1970).

Specific plant parts are selectively consumed by a large number of herbivores. This is a "behavioral" adaptation to the selection of plant parts that may be most appropriate for the anatomy and physiology of the species. Hoffmann (1973) grouped East African ruminants into three major classes based upon gastrointestinal anatomy and feeding habits. Others have extended these categories to additional herbivores.

Herbivores designated as "concentrate selectors" consume plant materials that are relatively low in plant cell walls. These concentrate selectors do not use large amounts of dietary plant fiber effectively and thus selectively feed on those plant parts that are higher in readily fermentable carbohydrates. Herbivores which consume plants that are relatively higher in cell wall components, typically grasses, are classified as "bulk and roughage eaters". The third class consists of "intermediate feeders" that are more adaptable to changing habitats and vegetation than most of the concentrate selectors and bulk and roughage feeders. Opinions differ as to which group is more highly developed. Among ruminants, concentrate selectors are commonly considered the most conservative (Van Soest, 1982). However, the ability of a ruminant species to tolerate and use the end-products of rapid fermentation, as seen in concentrate selectors, might also be considered as more recently evolved.

Primates as Herbivores

The differences in digestive tract anatomy associated with the three classes of herbivores above also can be found within the order Primates. Further, five categories of dietary adaptation can be defined: faunivory, exudivory, granivory, frugivory, and folivory, the latter two representing specializations of herbivory.

Primates which specialize in consuming leaves exhibit several gastrointestinal adaptations. Microbial fermentation occurs in the large sacculated forestomach of Colobidae (e.g., *Colobus* spp., *Presbytis* spp., *Trachypithecus* spp., *Pygathrix nemaeus*, *Nasalis larvatus*). Hindgut fermentation, in the sacculated cecum and/or colon, occurs in certain other primates (e.g., *Alouatta* spp., Indriidae). However, the extent of herbivory demonstrated by a given species is variable. Eisenberg (1978) described five classes or degrees of herbivory:

Class 1. Digestive tract shows little modification; dentition little modified for grinding; essentially omnivorous, but much "fruit" is utilized when available; some feeding on buds or shoots may occasionally be seen.

Class 2. Digestive tract shows little modification for bacterial symbionts. Dentition may show slight modification for grinding or crushing. In addition to some animal food, often feeds on plant parts including seeds, fruit, buds, flowers, leaves, and sap.

Class 3. Digestive tract shows some modification, generally, cecal enlargement and/or lengthening of the intestine. Dentition may show cusp modification to create crushing

surfaces. Diet differs from Class 2 in that buds, blossoms, leaves, and young shoots begin to dominate in the diet (from 30 to 40 percent). If terrestrial, the species may ingest occasional grasses/forbs, as well as leaves. such adaptation

Class 4. Digestive tract further modified from Class 3. Stomach is often very enlarged and sacculated or cecum is greatly enlarged. Some bacterial digestion of cellulose in the stomach is implied. Leaves and grass comprise a significant percentage of the diet (greater than 40 percent) although blossoms, fruit, and other plant parts contribute to the diet. If terrestrial, the species may be considered either a browser or grazer, depending on the proportion of leaves in its diet.

Class 5. Differs from Class 4 in that the species, if arboreal, is close to being an "obligate" folivore. Gut is specialized for the breakdown of cellulose by bacteria and/or protozoan symbionts. Leaves, buds, and plant stems predominate in the diet. Specimens of arboreal forms taken as advanced juveniles or older for captive rearing are almost impossible to convert to an artificial diet. If terrestrial, the species is generally a specialized browser or grazer.

It has been demonstrated that free-ranging primates do

not eat plant materials at random, but show decided preferences (Milton, 1984). Selective consumption of plant parts, which may be lower in structural carbohydrates, lignin, and/or secondary plant metabolites may be one such adaptation (Oftedal, 1991). Milton (1978a) suggested that the mantled howler monkey (*Alouatta palliata*), as a "behavioral folivore", utilizes this approach to folivory, consuming young leaves, fruits, and flowers from a diverse number of plant species.

It is difficult to generalize the feeding habits of primates whose diet consists, in part or entirely, of leaf material. Indeed, within the order Primates, a wide range of folivory is demonstrated. Much of this variation is reflected in the gastrointestinal anatomy of these species.

The colobine stomach has four parts: the presaccus and saccus, the long tubus gastricus, and the short pars pylorica (Kuhn, 1964). The large, complex presaccus and saccus are distended and sacculated proximally, with a U-shaped tube distally, and sacculated along the proximal part of the greater curvature (Hill, 1958). The sacculations seen in this region of the gastrointestinal tract are a result of longitudinal muscles, which have been reduced to two or more bands (taenia) (Chivers and Hladik, 1980).

Some variation in gut structure is seen with the subfamily Colobinae (Chivers, 1994). The stomach of the African colobines (e.g., *Colobus*, *Procolobus*) is more

elongated, with the tubular portion bent back on the saccular portion. Asian colobines (e.g., *Pygathrix*, *Presbytis*, *Nasalis*) have a saccular portion which is roughly spheroidal. In both groups, the hindgut is comparable, with a long sacculated colon and cecum of moderate size. Drawings of two colobine gastrointestinal tracts, the black and white colobus (*Colobus guereza*), and northern douc langur (*Pygathrix nemaeus nemaeus*) are given in Figures 1-1 and 1-2, respectively.

The presence of microbial organisms (Bauchop, 1971) and extensive microbial fermentation (Kuhn, 1964; Bauchop and Martucci, 1968) in the presaccus and saccus demonstrate the ruminant-like digestion possessed by colobine primates. The pH of the colobine foregut has been reported to be between 5.0 and 6.7 in langurs (Bauchop and Martucci, 1968) and 7.0 in colobus (Kuhn, 1964). Interestingly, although significant numbers of cellulolytic (e.g., *Bacteroides* spp.) and methanogenic (e.g., *Methanobacterium ruminantium*) bacteria are present in the foregut, protozoa have not been reported. It should be noted that there may also be considerable microbial fermentation in the cecum and colon of colobines (Milton and McBee, 1983; Ullrey, 1986).

The stomach of *Alouatta palliata* exhibits a great deal of complexity when compared with other cebids. The globular sac is capacious and narrows to the bent tubular pylorus. This portion of the stomach is guarded by strong pillars, and

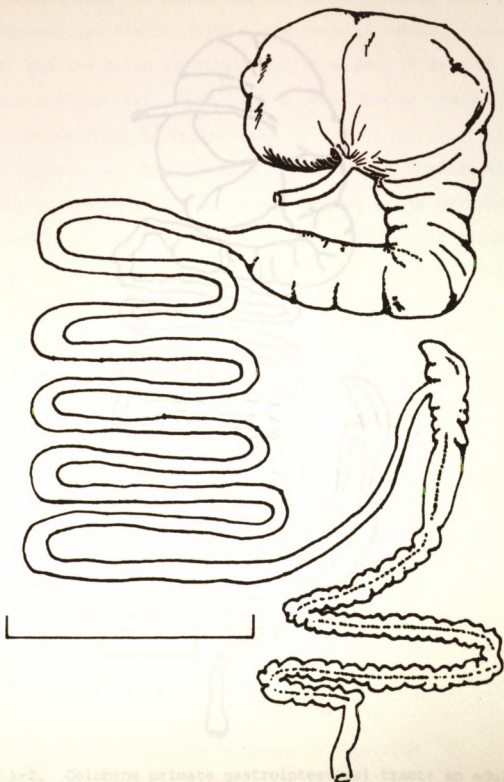


Figure 1-1. Colobine primate gastrointestinal tract: an adult, black and white colobus (*Colobus guereza*), body length = 50 cm, re-drawn from Stevens (1988). Scale equals 20 cm.

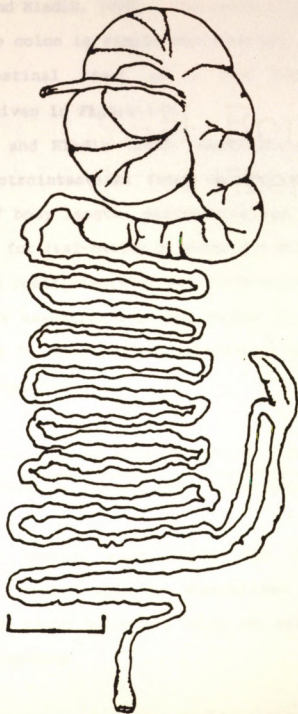


Figure 1-2. Colobine primate gastrointestinal tract: an adult (3 yr), female northern douc langur (*Pygathrix n. nemaeus*), body length = 52.0 cm, body weight = 6.09 kg, drawn directly from a photograph by Edwards. Scale equals 11 cm.

rugae radiate from the cardia and run longitudinally with the body (Chivers and Hladik, 1980). The cecum of cebids is hook-shaped, and the colon is simple and straight. A drawing of the gastrointestinal tract of a red howler (*Alouatta seniculus*) is given in Figure 1-3.

Chivers and Hladik (1980) conducted a quantitative analysis of gastrointestinal tract morphology in primates. Measurements of body length, gastrointestinal tract surface area and volume for leaf-eating primates are provided in Table 1-2. They used *coefficients of gut differentiation* (CGD) to make comparative assessments of the degree of specialization of a species for folivory. These values were determined using the following equation:

$$\text{CGD} = \frac{\text{surface area of stomach} + \text{cecum} + \text{colon}}{\text{surface area of small intestine}}$$

Those species with higher CGD values have a gastrointestinal tract that is specialized for microbial fermentation of plant material, with an enlarged stomach and/or large intestine.

Brief History of Folivorous Primates in Captivity

Numerous references, as early as 1892, to maintenance of captive folivorous primates in zoological institutions

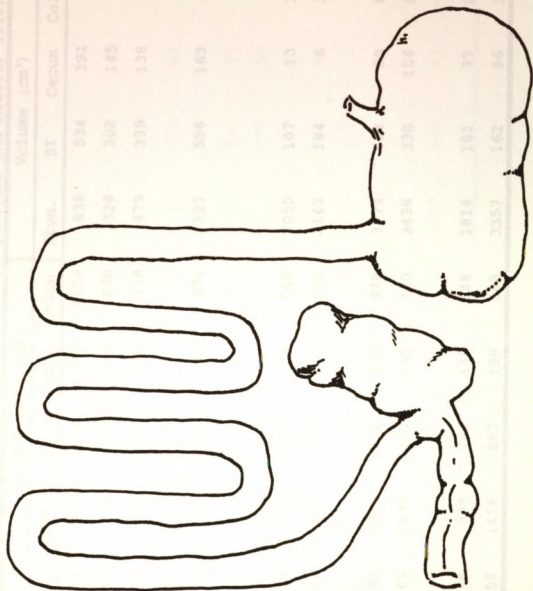


Figure 1-3. Cebid primate gastrointestinal tract: an adult, red howler (*Alouatta seniculus*) drawn from measurements and descriptions given by Crissey et al. (1989).

Table 1-2. Measurements of body length, and surface area and volume of stomach, small intestine, cecum, and colon in howler and colobine monkeys (Chivers and Hladik, 1980)

Species	Sex	BL (cm)	Surface area (cm ²)				Volume (cm ³)			
			Stom.	SI	Cecum	Colon	Stom.	SI	Cecum	Colon
<i>Alouatta</i>	M	51	430	1052	289	1059	839	534	391	959
<i>palliata</i>	M	50	230	719	148	630	328	302	145	471
	F	53	296	815	156	778	479	339	138	642
<i>Alouatta</i>	M	61	180	1106	150	578	227	556	163	422
<i>seniculus</i>										
<i>Colobus</i>	F	56	1021	556	26	549	2055	107	13	218
<i>polykomos</i>	F	58	1056	925	15	630	2162	184	6	301
<i>Presbytis</i>	M	63	1585	1673	105	978	3974	633	80	845
<i>entellus</i>	M	65	1439	1167	140	760	3438	330	104	505
<i>Presbytis</i>	F	48	938	740	139	548	1814	181	77	275
<i>senex</i>	M	59	1416	687	139	548	3357	162	96	336

Table 1-2 (cont'd). Measurements of body length, and surface area and volume of stomach, small intestine, cecum, and colon in howler and colobine monkeys (Chivers and Hladik, 1980).

Species	Sex	BL (cm)	Surface area (cm ²)				Volume (cm ³)			
			Stom.	SI	Cecum	Colon	Stom.	SI	Cecum	Colon
<i>Presbytis</i> <i>cristata</i>	F	50	1694	1929	90	966	4831	604	64	645
	F	53	1175	1329	30	607	2209	385	12	285
<i>Presbytis</i> <i>obscura</i>	M	50	1363	1953	64	670	3237	699	41	343
	F	45	956	1311	52	558	1788	397	27	264
<i>Presbytis</i> <i>melalophos</i>	M	53	1351	1969	88	902	2974	734	51	588
	F	56	1282	1129	90	869	3139	327	64	546
<i>Presbytis</i> <i>melalophos</i>	M	51	1020	1386	60	532	2072	336	34	156
	M	44	694	1075	23	369	1128	247	8	132
<i>Presbytis</i> <i>melalophos</i>	F	47	1648	1796	60	552	3521	517	36	224
	M	49	1078	1389	42	695	2158	395	20	362
<i>Presbytis</i> <i>melalophos</i>	F	50	1382	1695	68	848	3327	588	43	469
	F	52	1274	2021	38	512	2296	633	14	292

Table 1-2 (cont'd). Measurements of body length, and surface area and volume of stomach, small intestine, cecum, and colon in howler and colobine monkeys (Chivers and Hladik, 1980).

Species	Sex	BL (cm)	Surface (cm ²)			Volume (cm ³)				
			Stom.	SI	Cecum	Colon	Stom.	SI	Cecum	Colon
<i>Prebytis rubicunda</i>	M	56	1125	1672	45	637	2259	505	20	329
<i>Nasalis larvatus</i>	M	64	1978	3120	100	1234	6523	1127	66	655
<i>Pygathrix nemaeus</i>	F	53	1243	1512	36	578	2960	444	12	261
	F	60	1431	1601	80	854	3442	531	42	433

exist in the literature. Success in maintaining populations of folivorous primates in captivity has been widely mixed, and to date, is highly related to species (Collins and Roberts, 1978). Mitchell (1911) reported the average life-span of six species of captive langurs ($n=56$) as 4.3 months (mos), with the maximum being 15 mos. In 1967, the longevity record for the northern douc langur (*Pygathrix nemaeus nemaeus*) in captivity was reported to be 4 mos at the London Zoo (Hick, 1972). Meritt (1982) reported "longevities" of a few mos for both red (*Alouatta seniculus*) and black howlers (*A. caraya*) received at the Lincoln Park Zoo (Chicago) in the late 1960s. Although Crandall (1964) described the black and white colobus (*Colobus polykomos* = *guereza*) as a very difficult subject to maintain in the zoological garden and Flower (1931) indicated the "African colobus or guereza monkeys appear to be even more difficult than the langurs to keep alive in captivity", this species has proven to be the most adaptable folivore in captive environments. In 1927, a single specimen of black and white colobus was maintained for 3 years, 24 days in the New York Zoological Park (Crandall, 1964). Even though this record seems hardly worthy of mention, at that time this animal held the longevity record. Currently, black and white colobus regularly live beyond 20 years in zoological collections (Jones, 1995). By 1971, births of third generation captive offspring were being reported (Hollihn,

1973).

Species differences in dietary habits in the wild and in the morphology of the gastrointestinal tract suggests that all captive primates should not be fed in the same manner (Ullrey, 1986). The importance of a diet that delivers higher fiber concentrations has been alluded to by several authors. Success in adapting wild-caught colobines to captive conditions is reported to be dependent upon the conditions in which the monkeys are kept immediately following capture (Hollihn, 1973; Lindbergh, 1976; Eisenberg, 1978). Urbain et al. (1955) suggested that black and white colobus could not survive in captivity without an abundance of leaves of the vine *Vitis vinifera*, mulberry (*Morus alba*), or aucuba (*Aucuba japonica*). These authors point to an "essential element" provided by these plant species which is not present in cultivated vegetables, fruits, or greens. Additionally, an increased frequency of feeding (i.e., six times daily) in conjunction with appropriate dietary components was suggested as an effective method of dietary husbandry (Ludwig, 1989).

Crandall (1964) indicated that problems surrounding the captive husbandry of howler monkeys could be solved, in part by a diet providing sufficient leafy bulk. Although no attempt has been made to identify the "essential elements" that should be present in the diet of folivores, the contribution of appropriate levels of plant fiber should not

be overlooked.

The development of diets for captive wild animals has historically been one of trial and error. An animal's basic feeding preference (e.g., herbivore, frugivore, omnivore) is a simplistic, but common starting point. Commercially available substitutes for food types selected by wild specimens have been offered to determine acceptance. Unfortunately, this approach placed a great deal of reliance upon "nutritional wisdom", a concept that has been declared invalid for wild animals in captivity (Ullrey, 1987). Although bearing similar names (e.g., fruits), the nutrient composition of cultivated plant foods is generally quite different from that of plant foods consumed in the wild (Edwards, 1990). Many animal managers have sought the "secret ingredient" that allows a species to thrive in captivity. However, with few exceptions, controlled studies have demonstrated that animals require specific nutrients, not specific ingredients.

Although the specialized feeding habits of leaf-eating primates have long been recognized by individuals attempting to maintain them in captivity, systems of dietary husbandry are still widely variable. In fact, folivorous primates are often fed diets that are similar to those fed to primate species that are not primarily folivorous and/or do not have pregastric fermentation (Hollihn, 1973; Watkins et al., 1985).

This has resulted in a high incidence of gastrointestinal disorders (Hill, 1964; Hick, 1972; Hollihn, 1973; Benton, 1976; Benirschke and Bogart, 1978; Heldstab, 1988; Taff and Dolhinow, 1989; Janssen, 1994).

The diversity of ingredients and diets offered to captive folivores is remarkable. The following diets were listed by Crandall (1964):

Angola colobus (*Colobus angolensis*), per animal, daily:

- Lettuce, 1 head
- White potatoes, raw, 8
- Sweet potato, raw, 1
- Carrots, raw, 4
- Bananas, 2
- Peanuts, whole, 25
- Bread, rye or raisin, 4 slices
- Reconstituted evaporated milk with coddled egg, 1/2 pt
- Baby cereal
- Cod-liver oil, 1/2 tsp
- Celery, leaves of bamboo, and Russian mulberry, when available

Mantled howler (*Alouatta palliata*), per animal, daily:

- Milk gruel (reconstituted evaporated milk, thickened with cooked, rolled oats or Pablum™, with 2 drops of multiple vitamin concentrate added)
- Cabbage, raw, 1/2 head
- Bread, raisin, slices, 3
- Carrot, 1
- Celery, stalks, 3
- Egg, hard-boiled, 1
- Grapes, 1 dozen
- Apple, 1
- Dog food, canned, 1 oz
- Milk gruel, 8 oz (prepared as above)

Interestingly, despite the obviously inappropriate nature of the above diets and some of the ingredients, the author (Crandall, 1964) urged caution concerning the feeding of

certain items, such as oranges or orange juice, which were believed to produce severe diarrhea in these animals. This specific concern for excessive use of citrus was reiterated by Merrit (1982). Hollihn (1973) emphasized the importance of leaf material in the diet of colobine primates, and cautioned against the feeding of "easily digestible carbohydrates and fats" such as rice, bread, and nuts. Yet, in the same article, this author promoted the feeding of unpeeled fruits such as bananas, melons, and citrus fruits as a source of "ballast substances" that are "plentiful in the natural diet". Further, Hick (1972) listed the diet of douc langurs housed at the Cologne Zoo as including "a ration of cooked rice, fruits, vegetables, rose leaves, and willow twigs" which, as with Hollihn's (1973) description, included food items that are both relatively high in readily fermentable carbohydrates and in plant cell wall. Additionally, Hick (1972) indicated that the douc langurs were provided with black tea, for drinking in the morning hours, and boiled water in the evening.

These apparent inconsistencies are not limited to the dietary husbandry of colobines. Benton (1976) cited the importance of diet as a primary variable upon which the success of captive groups of howler monkeys (*Alouatta* spp.) rests. The author noted gastrointestinal adaptations of howler monkeys, including a "semi-sacculated" stomach, which enable members of this genus to "cope with the vast

quantities of high bulk vegetable matter normally consumed in the wild". Despite this background information, the diet fed to these animals included the following, in the morning:

- Evaporated milk (227 g) mixed with an equal quantity of water, boiled and mixed with:
- Soft-boiled eggs
- Gevral™ protein powder (protein supplement)
- Lactinex™ tablets (*Lactobacillus acidophilus*)
- ABDEC™ vitamin drops
- Clovite™ capsules
- Farbegen™ capsules (iron supplement)

This mixture was then poured over:

- Fresh white bread, to form a semi-solid gruel

The evening feeding, offered in two courses, included:

- Boiled chicken
- Fruit-flavored yogurt
- Soft-boiled eggs
- Purina Monkey Chow™ (25% crude protein) soaked in tea
- Raisins
- Peanuts
- Sunflower seeds
- Celery
- Tomatoes
- Carrots
- Apples
- Plantains
- Canned figs
- Grapes
- Blueberries
- Strawberries
- Fresh corn, on cob
- Leafy green matter (lettuce, cabbage, spinach, kale)

As available, additional items were fed, including:

- Papaya
- Mango
- Blackberries
- Canned dog food

The author noted that quantities of individual foods offered were not large enough to allow animals a daily portion of

every ingredient. However, he felt it was more important to prevent "dietary boredom" than to ensure that each individual had the opportunity to consume preferred foods. Although no water was provided to this group of animals, they were given boiled tea, double-strength, sweetened with honey and fortified with an additional protein supplement. This practice was similar to the recommendations of Hick (1972), and appears to be based upon the misconception that these arboreal primates in the wild strictly drink water that is high in tannic acid.

The importance the above authors placed on adherence to these diets and the myths surrounding them focused on the ingredients fed and not the nutrients provided or provision of a diet that approximated the composition of foods consumed by free-ranging animals.

Those institutions that seem to have the greatest success with long-term maintenance of captive folivorous primates are those that have addressed their specialized needs (Edwards, 1990). There are three primary methods of increasing the amount of fiber in these animals' diets. The most widely applied, and easily implemented approach, is the replacement of commercial primate biscuits containing a low concentration of fiber (10-19% NDF, 5-7.5% ADF) with a higher-fiber product (25% NDF, 15% ADF). The lower fiber commercial primate diets were designed originally for omnivorous

primates, such as macaques. The commercial production of higher fiber primate diets is a fairly recently available option, as zoo feed manufacturers respond to the scientific evidence and demands of the enlightened consumer.

Another approach includes the reduction or elimination of commercially available fruits and replacement of those items with leafy greens and higher fiber vegetable material. This method is often used in conjunction with the incorporation of the higher fiber primate biscuit.

The cultivation of plant material for supplemental feeding is also an option (Griner, 1977; Ullrey et al., 1982). This practice is not as widespread, due primarily to the variability of local growing conditions and economic considerations (Koontz et al., 1988). The types of plant material cultivated also are widely variable, from indigenous species to easily grown tropical plants. Surprisingly, no attempts have been made to cultivate widely the browse plants that are consumed by free-ranging representatives of the species held in captivity.

Special considerations should be taken when offering browse to captive primates. Nutrient contributions of the browse material should be determined (Mannchen, 1989), and the impact of seasonal variability and fertilization of browse plant materials should be assessed. Additionally, protective substances such as the secondary compounds previously

described can be present within these plants (Santi and Santi, 1989). The animals to which these plants are offered (most of which have been born in captivity) should be considered naive to such defenses and should be monitored as to the parts of the plants that are consumed. As this approach to feeding becomes more common, reports of deaths directly attributable to the consumption of browse have increased (Hill, 1964; Ensley et al., 1982; Robinson et al., 1982; Janssen, 1994; Edwards, unpublished data). This is an unfortunate demonstration of the evolutionary effectiveness of mechanisms that plants have developed to protect against herbivory, as well as the consequences of relying upon "nutritional wisdom" when offering naive animals novel foods.

An ideal approach to the feeding of captive folivorous primates appears to be a combination of the above three methods:

1. Use a higher fiber primate biscuit.
2. Reduce or eliminate fruits, and increase green leafy vegetables.
3. If browse plants are fed, ensure that they are appropriate.
4. Distribute these foods in small quantities over several feedings per day.

Chapter II

Feeding Habits and Nutrient Composition of Natural Diets of Free-Ranging Red Howler Monkeys (*Alouatta seniculus*)

Background

Howlers (Family, Cebidae; Subfamily, Alouattinae Elliot, 1904; Genus, *Alouatta* Lacepede, 1799) are large primates, with adults weighing, on average, between 7 and 9 kg (Fooden, 1964). These animals are the largest members of the New World primates (Platyrrhini). Seven species and sixteen subspecies of howler monkeys are currently recognized, including: *Alouatta belzebul* Linnaeus 1766, *A. seniculus* Linnaeus 1766, *A. caraya* Humboldt 1812, *A. palliata* Gray 1849, *A. fusca* Ihering 1914, *A. pigra* Lawrence 1933, and *A. coibensis* (Hill, 1962; Hershkovitz, 1969; Smith, 1970).

Howlers are the most widely distributed of all the Platyrrhini. These animals range from southern Mexico through Central America and northern South America, extending into Argentina and Brazil. This range covers a wide diversity of habitats including tropical rainforests of Panama and Brazil, cloud-forest regions of Venezuela and

Columbia, the deciduous forests of Guatemala, dry forests in Costa Rica, and llanos regions of Venezuela.

Howlers are highly arboreal primates. However, these animals will descend to ground level under certain conditions (Carpenter, 1934; M.S. Edwards, unpublished data). The tail of the howler is fully prehensile, with a naked patch of skin on the caudal surface of the tip. Howlers are named for their deep roaring call. Beneath the chin is a large swelling which is the site of the specialized hyoid bone. The hyoid bone is larger and more pronounced in the male of the species, but is also modified in the female.

Howler monkeys are considered to be the most folivorous primates within the infra-order Platyrrhini and are strict vegetarians (Carpenter, 1934; Fooden, 1964; Hladik and Hladik, 1969; Richard, 1970; Eisenberg et al., 1972; Smith, 1977; Eisenberg, 1978; Gaulin et al., 1980; Gaulin and Gaulin, 1982; Braza et al., 1983). Most of the published information concerning foraging behavior of howler monkeys has been obtained from the study of one species within the genus, the mantled howler monkey (*Alouatta palliata* = *Alouatta villosa*). This information has been collected from two localities, Panama, specifically Barro Colorado Island (Carpenter, 1934; Hladik and Hladik, 1969; Milton, 1978a; Milton, 1978b; Gaulin et al., 1980) and Costa Rica (Glander, 1975).

Based on data collected by Hladik and Hladik (1969),

Eisenberg described the mantled howler as a species whose digestive tract shows some modification towards herbivory, specifically cecal enlargement and/or elongation of the intestine (Class 3). This is supported by Fooden's (1964) description of the red howler gastrointestinal tract as possessing high ratios of organ length to body length for stomach, cecum, and large intestine. Further, the large diameter of the cecum was argued as hindgut modifications supporting microbial fermentation of a strictly vegetarian and rather folivorous diet (Fooden, 1964; Amerasinghe et al., 1971).

The natural diet is dominated by buds, blossoms, leaves, and young shoots. These plant parts are reported to contain lower quantities of structural carbohydrates, making them more digestible than mature leaves.

When compared to the mantled howler, described as a leaf/fruit-eating primate, the red howler appears to have similar feeding habits. However, many of these descriptions are based on either direct visual observation or gut content analysis. Milton (1978a) suggested that the lack of geographic overlap among the various species of *Alouatta* is the result of similar dietary niches.

Howler monkeys have been described as "behavioral" folivores rather than "anatomical" folivores (Milton, 1978a). This description is based on the observations and anatomical

adaptations of the mantled howler monkey on Barro Colorado Island, Panama. This description has been accepted as valid across the entire genus, primarily due to the lack of specific information concerning the composition of food items selected by or detailed examination of gastrointestinal anatomy of other species of howlers.

The objectives of this portion of the study were to examine the feeding habits of the red howler monkey (*Alouatta seniculus*) in the central llanos of Venezuela, including a detailed description of the red howler's natural diet. Calculations were made to determine nutrient intake based upon behavioral observations. Bite counts of plant parts consumed by free-ranging animals and direct measurements of bite weights of the same food plants offered to the same study subjects in captivity were used to complement the behavioral data. Nutrient analysis of specific parts of food plants selected was combined with these two estimates of intake to determine the nutrient profile of the consumed diet.

Limited information has been collected on the feeding habits of the other six species of howler monkeys. Little is known of the dietary habits of either *Alouatta belzebul* (Braza et al., 1983) or the black howler monkey (*Alouatta caraya*) (Pope, 1966; Bicca-Marques and Calegario-Marques, 1993). Carvalho (1975) listed the plants selected by *A. guariba*. Limited descriptions of the diet of the red howler monkey, the

species observed in this study, are available. These descriptions consist of information collected by direct field observations, gut content analysis, and scat analysis (Fooden, 1964; Izawa, 1975; Hernández-Camacho and Cooper, 1976; Braza et al., 1983). The most detailed dietary description for the red howler was provided by Gaulin and Gaulin (1982) for animals inhabiting the Colombian Andes cloud forest. This single study made estimates of plant material intake via visual observation, in contrast to the more conventional method of reporting the diet as a percentage of total feeding time. Regardless, the information collected on mantled howlers represents the majority of knowledge to date on the feeding strategies within the genus *Alouatta*.

A single male red howler was examined post-mortem by Racenis (1952). The stomach contents of this animal consisted primarily of Venezuelan ragweed (*Ambrosia cumanensis*). Racenis (1952) reported that this plant grows in large quantities on the banks of the Orinoco river, where his study was located.

The red howler monkeys found in the basin of the river Caqueta were reported to consume leaves of unidentified trees, the fruit of *Pourouma* spp., and beans which were similar to the nuts of *Pakia oppositifolia* (Izawa, 1975). These observations were made on six separate occasions between December 1971 and September 1973. The amount of time that the

animals spent feeding and other specific information, such as time spent resting and moving, were collected in this study.

Braza et al. (1983) examined the feeding habits of the red howler monkey in the llanos of Venezuela. Their analyses of the gut contents of howler monkeys identified leaves, of an undetermined phenological stage, in 73.8 % of the stomachs examined. Fruits also were found in 73.8% of the stomach contents, whereas legume pods were found in 21.3% of the stomach contents. The limitations of gut content analysis have been discussed by numerous investigators. Gut contents provide a view only of a "single meal", since they represent only those foods selected shortly before the animal's death. There may be some difficulty in identifying plant species which have undergone mastication and partial, or extensive, peptic digestion in the stomach. Finally, the animals must be killed to conduct such an analysis, thus limiting the potential sample size.

Fecal (scat) analyses also have been conducted to determine the feeding habits of the red howler of the llanos (Braza et al., 1983). The results of these analyses indicate that leaves were found in 95.3 %, fruits in 83.2 %, and woody stalks in 64.2 % of fecal samples examined. Fecal analysis is the most noninvasive method of determining the feeding habits of a given species, but feces represent only the end-products of digestive processes (Moreno-Black, 1978). Food

items which can be identified in the scat sample are typically those which are the most resistant to digestion. This fact may explain the high proportion of woody stalks in the feces, when only 18.0% of the stomach contents contained such material. Additionally, an extensive reference collection of plant materials is required to conduct fecal analyses with accuracy.

An interesting finding of Braza et al. (1983) was the presence of grasses both in stomach contents (4.9 %) and in fecal samples (0.8 %) collected from the howlers of the llanos region. Although, it is known that these animals will descend to the ground for travel and to obtain water (Racenis, 1952; Edwards, unpublished data), direct observations of the consumption of grasses by red howlers have not been reported. Therefore, it seems unlikely that ground vegetation would constitute a dominant portion of the howler's diet (Braza et al., 1983).

Gaulin and Gaulin (1982) reported quantitative estimates of food intake based upon visual observations of red howlers. This method was used in combination with collection of the various foods selected. These estimates were based upon the number of food items consumed per "feeding bout" and then multiplying the number of items by the mean weight of the item. For example, they determined that the mean fresh weight of a mature leaf of *Ficus cundinamarcensis* is 2.57 g. If an

animal consumed seven of these leaves in a feeding bout, they computed that the animal ate 7×2.57 or 17.99 g of plant material, as fed basis.

Colobine monkeys (e.g., *Presbytis* spp., *Trachypithecus* spp., *Pygathrix nemaeus*, *Colobus* sp.), which are Old World species, have highly specialized, large sacculated foreguts that permit extensive fermentation of digesta by symbiotic microbes (Hill, 1962). This gastrointestinal arrangement is similar to that of ruminant artiodactylids; however, the colobine primates do not ruminate. The absence of rumination is critical when examining the feeding strategy of these animals. Fermentation by microorganisms in the gastrointestinal tract of these animals or in ruminants is unable to degrade the lignin in plant cell walls. Ruminants are able to reduce the particle size of this polyphenolic compound through remastication of food during rumination. Without a reduction in physical size, the lignin fibers may become entwined, forming fibrous "ropes" called phytobezoars. These phytobezoars may obstruct the gastrointestinal tract of colobines, and physically block the passage of digesta through the gut (Ensley et al., 1982; Edwards, unpublished data).

Howlers have been described as the New World analog of the Old World folivores (Hill, 1962; Hladik and Hladik, 1969; Richard, 1970; Eisenberg et al., 1972; Jolly, 1972; Eisenberg and Thorington, 1973). Howlers lack the foregut

specialization of colobines and appear to depend on an expanded cecum and colon (Amerasinghe et al., 1971; Crissey et al., 1989) as a site where fermentation processes occur. However, the significance of this adaptation for utilization of fiber has been disputed (Milton, 1980).

The red howler monkey is abundant and widely distributed throughout Venezuela (Bodini and Perez-Hernandez, 1987), and ranges into neighboring Colombia, Guiana, Bolivia, and the Amazon basin and Atlantic coastal regions of Brazil. Red howlers are extremely adaptable and are found in a wide array of habitats within Venezuela, including montane forests, rain forests, and deciduous forests. Hill (1962) described three subspecies of *A. seniculus* in Venezuela (*Alouatta seniculus seniculus* Linnaeus, *A. s. arctoidea* Cabrera, and *A. s. stramineus* Humboldt). A fourth, previously unrecognized subspecies which inhabits the Venezuelan llanos, has been described (Bodini and Perez-Hernandez, 1987). This previously undescribed subspecies was identified by its coloration and size. Based upon genomic rearrangements, Stanyon et al. (1995) placed this subspecies among *Alouatta seniculus arctoidea*.

Materials and Methods

Study Area

The field work portion of this project was conducted

during a 16-mo period from August 1987 through December 1988 in the central llanos of Venezuela. The llanos comprise a band of savannas extending from the base of the Andes mountains eastward to the Orinoco basin and the Atlantic ocean. The study site was located on a private ranch, Hato Masaguaral, at approximately 8° 34' N, 67° 35' W. Figure 2-1 describes the location of Hato Masaguaral within the political boundaries of Venezuela.

The study site was located approximately 2 km south of the ranch houses. This area was a recently acquired portion of the ranch and had not been previously used for studies of red howlers. Hato Masaguaral covers an area of approximately 5,702 hectares. Figure 2-2 shows the location of the study site in relation to the ranch houses and the sites of previous red howler research at the ranch (Rudran, 1979; Crockett, 1985).

Climate and Photoperiod

The llanos are in a region of dramatic seasonal changes. The 6 mo of rainfall (May through October) constituting the wet season are flanked by 2 transitional mo (April and November) (Table 2-1). The marked dry season, which begins in December, often extends into May. Although this is the typical pattern, both the duration and amount of rainfall are extremely variable (Troth, 1979).

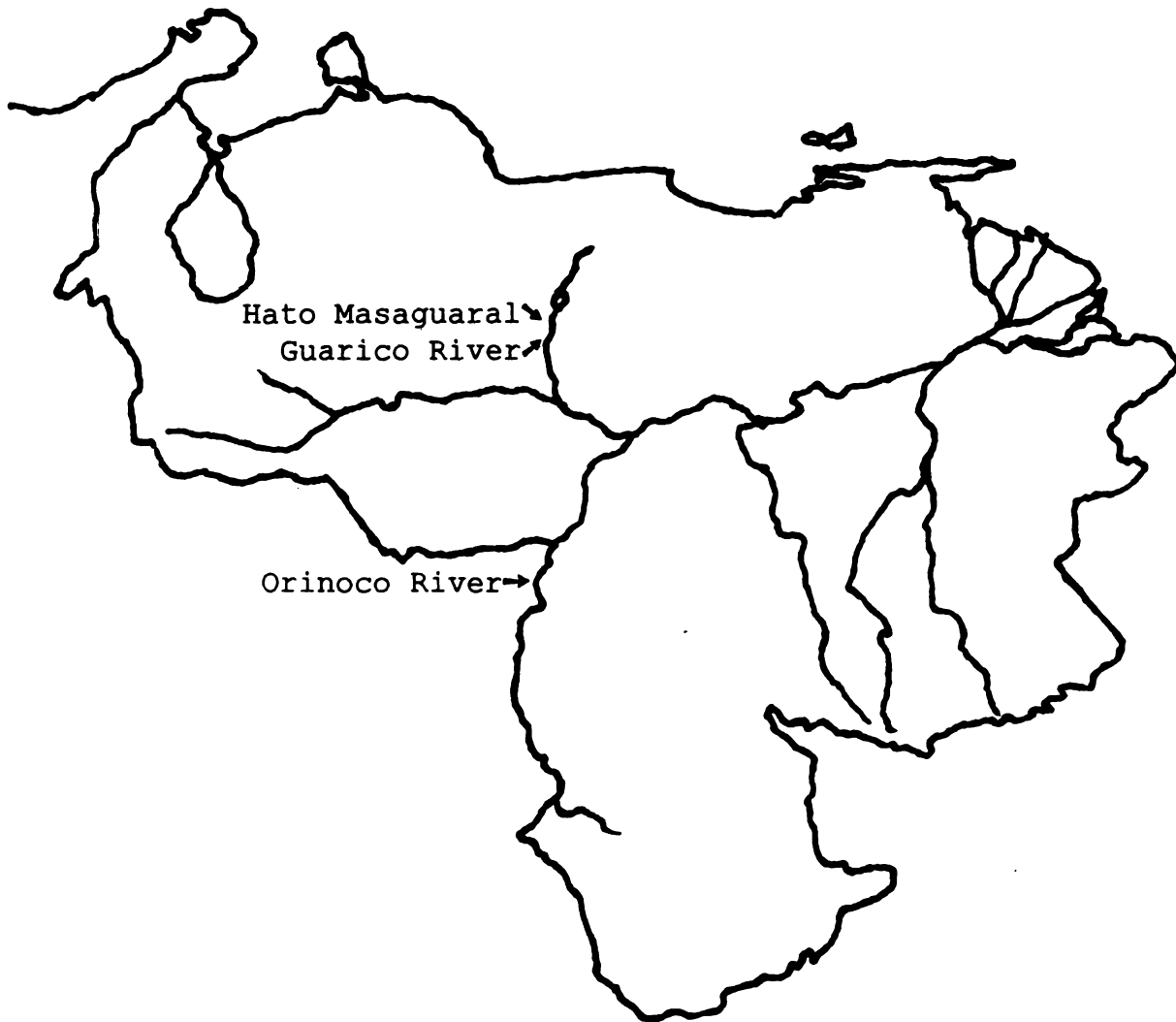


Figure 2-1. Political map of Venezuela with location of field study site (Hato Masaguaral).

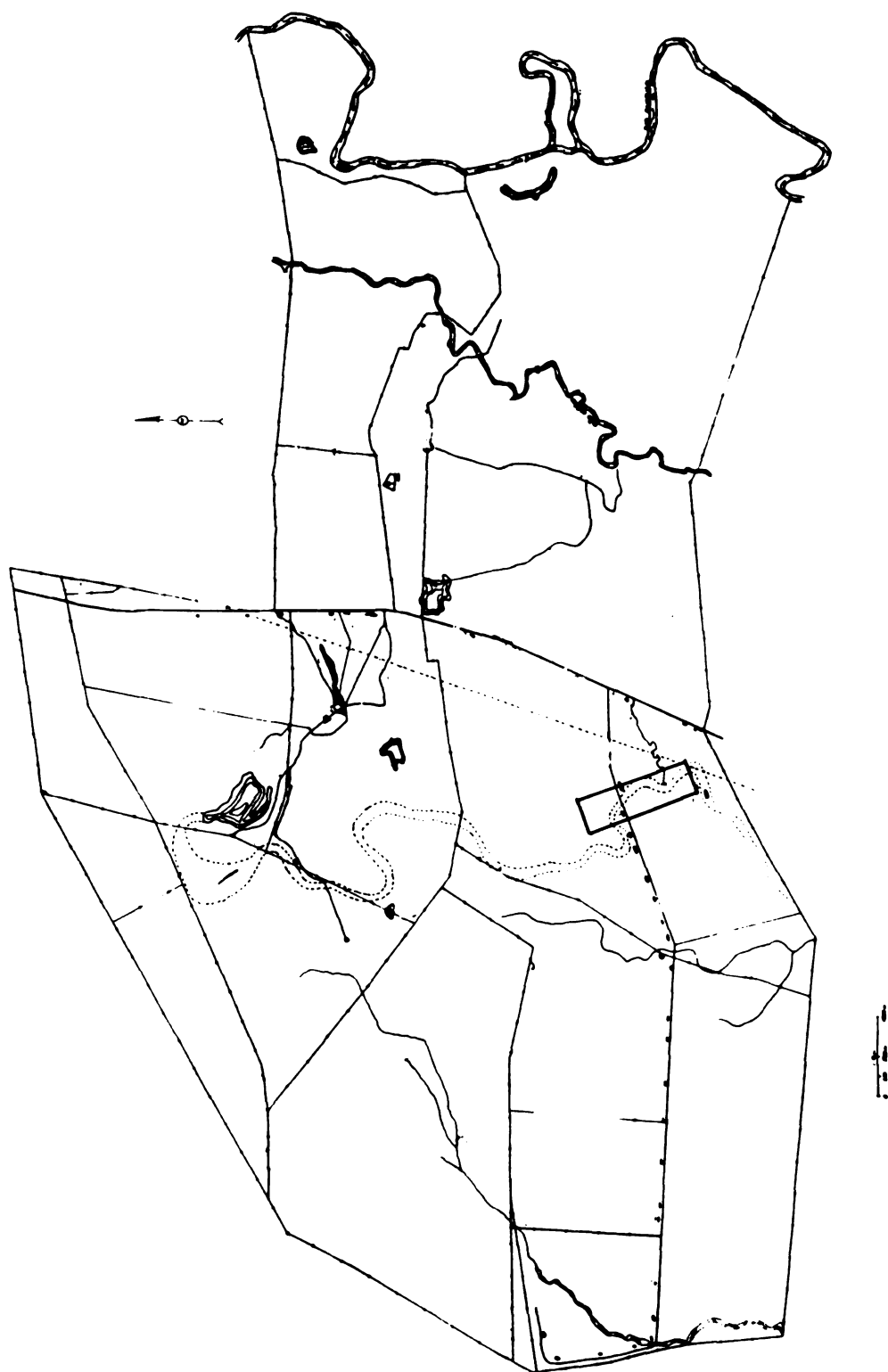


Figure 2-2. Map of Hato Masaguaral with location of study area in box. Scale equals 1 km.

Table 2-1. Summary of total annual precipitation for Corozo Pando, a village 8 km south of Hato Masaguaral.^a

Year	Amount (mm)	Mo with $\geq$ 50 mm
1953	2041	8 (April-November)
1954	1535	8 (April-November)
1955	1829	8 (April-November)
1956	1453	6 (May-October)
1957	1152	7 (May-November)
1958	1588	6 (May-October)
1959	1084	7 (May-November)
1960	1495	9 (April-December)
1961	1167	6 (June-November)
1962	1600	6 (May-October)
1963	1822	8 (April-November)
1964	1346	8 (April-November)
1965	1549	7 (May-November)
1966	1510	8 (May-December)
1967	1515	6 (May-October)
1968	1347	7 (May-November)
1969	2284	10 (February-November)
1970	1555	7 (May ? -November)
1971	938	7 (April ? -October)
1972	888	7 (April-October)
1973	1424	8 (April-November)
1974	1272	6 (May-November)
1975	1350	7 (May-November)
1976	1743	8 (April-November)
1977	ca. 1070	7 (May-November)

^aTroth, 1979.

Little variation in the temperature is observed annually (Figure 2-3). However, the greatest diurnal differences as well as the maximum and minimum annual temperatures occur during the dry season (Troth, 1979).

The photoperiod at this latitude is relatively consistent. A 12-hr daylight period is present year-round. However, there is an approximate 0.5-hr shift in dawn and dusk between seasons.

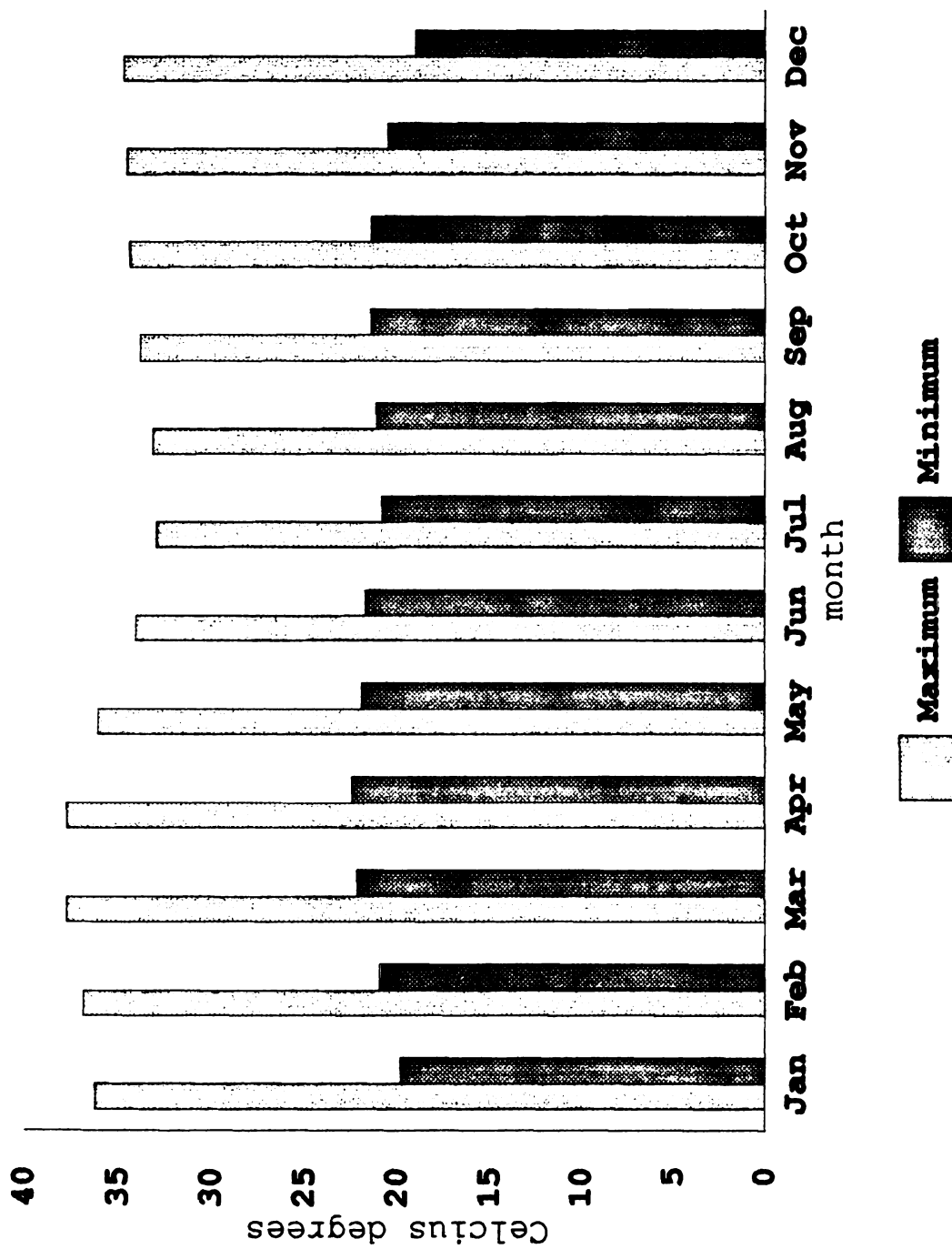
Vegetation Types

The vegetation found in the llanos is well adapted to the cyclic availability of water. The vegetational types in the savanna of Hato Masaguaral have been described as Medano (sandhill), Banco (non-flooded, low ridge), Bajío (moderately flooded savanna), and Estero (more deeply flooded savanna) (Troth, 1979). Additionally, Troth (1979) categorized gallery forest as the fifth major habitat found on the ranch. The study site included three of these five habitats.

Banco. These areas consist of low ridges which follow the course of old waterways. Troth (1979) stated that "the soils are composed of heavy particles. These areas are never truly flooded, but shallow puddles can be found there during the height of the rainy season. The woody vegetation is very open and is dominated by the common palm (*Copernicia tectorum*).\" Associated with many of these palms are strangler figs (*Ficus* spp.)

Bajío. This is the most common vegetative zone found on the ranch. The woody vegetation of this moderately flooded savanna is dominated by the common palm and associated

Figure 2-3. Average maximum and minimum temperatures (Estacion Biologica, SVCN) (Troth, 1979).



strangler figs. Additionally, several shrub species are found in this zone. Clusters of woody vegetation are found in the bajío forming "islands" within the savanna and are known as matas.

The vegetation of the shrub woodland bajío forms a shrub cover which can be so extensive that the canopy can be 90-100 percent closed. The tree layer of this habitat type is 8-15 m high and the shrub layer is 2-10 m high (Troth, 1979). Several species of herbaceous vines and lianas are found in this region.

Estero. This is the more deeply flooded habitat zone. This region is lacking in woody vegetation, with the exception of an occasional palm (*Copernicia tectorum*) or shrub (e.g., *Annona janhii*). The water depth during the peak of the wet season varies from 20-60 cm but may reach a depth of 110 cm (Troth, 1979).

Plant Identification

The vascular plants found within the perimeter of Hato Masaguaral have been previously cataloged (Troth, 1979). However, the study site was located in an area of the ranch which had not been surveyed. Consequently, some species which had not been included in the initial surveys were identified. Numerous sources were utilized, many in combination, in the identification of these plants, including popular texts (Hargreaves and Hargreaves, 1960; Hargreaves and Hargreaves, 1965), keys (Ramia, 1974) and personal communication with colleges on-site and local residents.

Behavioral Observations

Studies of arboreal primates are often inhibited by the dense vegetation in which the animals are found. Keeping

focal animals or other members of the study group continuously in view is difficult, if not impossible, under most field conditions. Investigators studying free-ranging animals have attempted to solve this problem by using a variety of sampling techniques (Chalmers, 1968; Chivers, 1969; Aldrich-Blake, 1970; Richard, 1970; Beck and Tuttle, 1972; Glander, 1975).

The habitat/vegetation types found within the area of this study were integral to the success of the behavioral observations. There was little difficulty in keeping the focal subject in full view due to the relatively low canopy and the absence of a vegetation zone at mid-story, allowing an unobstructed view.

These field observations were conducted from August 1987 through December 1988. The first 2 mo were spent locating a suitable study site, selecting two study groups, identifying plant species within the study site, and finalizing the methodology. The territories of the two study groups were adjacent to each other, and the habitat types found in both areas were essentially identical in composition. Figure 2-4 describes the study site and territories of the two study groups.

In an attempt to decrease variability, the two groups of red howlers selected for the project were of similar size and composition (e.g., sex ratio, age ratio). Further, each group possessed a single adult male, which was an additional

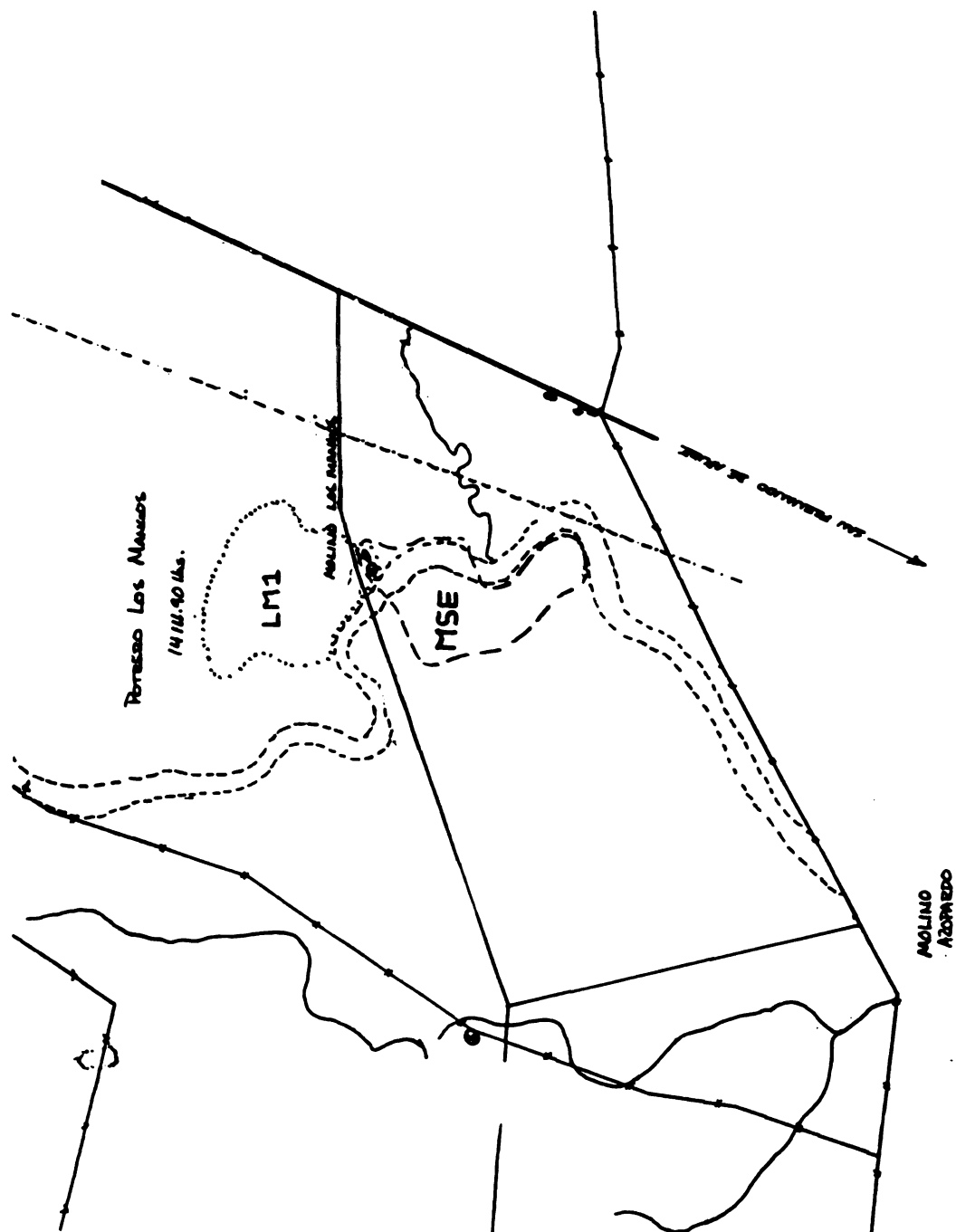


Figure 2-4. Study site and estimates of study group (MSE, LM1) territories.

selection factor necessary for the second phase of this project. The animals were identified by using existing physical characteristics, scars, and missing digits. The composition of each group, MSE and LM1, is given in Table 2-2. On July 6, 1988, a male infant (σ^3) was born into group LM1. A subadult/adult male (σ^2) left group LM1 in October, 1988.

Table 2-2. Demographic composition of two red howler monkey study groups.

Group ID	Animal ID	Age class ¹	Specific marks
MSE	σ	Adult	
	$\text{♀}1$	Adult	
	$\text{♀}2$	Adult	
	σ^{juv}	Juvenile	
	♀^{inf}	Infant	
	σ^{inf}	Infant	
LM1	σ^1	Adult	Cut on lower R lip
	σ^2	Sub-Adult	
	$\text{♀}1$	Adult	Missing upper incisor
	$\text{♀}2$	Adult	Scar on upper R lip; notch in R ear
	$\text{♀}3$	Juvenile	
	$\text{♀}4$	Infant	$\text{♀}1$'s infant
	σ^3	Infant	$\text{♀}2$'s infant

¹Age class determined upon initiation of study or upon birth of an individual.

During the first 2 mo of the study, the animals were

gradually habituated to the presence of an observer. Since the ranch was closed to hunting, and contact with humans (ranch workers) was fairly regular, the habituation process was quite rapid. A similar response of red howlers to human presence was reported by Racenis (1952). Both study groups were habituated to approaches within 5 m on foot by the onset of formal observations in October 1987. Toward the end of the study, several individual animals would allow observers to approach within 2 m.

An observation period was established during the first 2 wk of each mo. The animals were observed in a semi-random manner which included watching each animal once daily during a different time block. At the end of the month's observation period, a composite day could be constructed for each animal from the time blocks. The animals were randomized again each mo. Table 2-3 provides an example of a typical month's observation schedule for a group. The groups were located through late afternoon census surveys the day immediately preceding the observation series. Each animal was observed for 12 h each mo, from approximately 0630 to 1830 h. This corresponded to the entire daylight period and varied slightly with seasonal changes in dawn/dusk. This schedule helped to decrease the bias created by days of continuous rain, during which the animals were relatively inactive.

The animals selected a specific tree in which to sleep

Table 2-3. Example of a single month's observation schedule for MSE group.

Time	MON	TUE	WED	THR	FRI	SAT
06:30-08:30	♀2	♂	♂inf	♀1	♂juv	♀inf
08:30-10:30	♂juv	♀1	♀2	♂	♀inf	♂inf
10:30-12:30	♂	♀inf	♀1	♂juv	♂inf	♀2
12:30-14:30	♀inf	♀2	♂juv	♂inf	♀1	♂
14:30-16:30	♀1	♂inf	♀inf	♀2	♂	♂juv
16:30-18:30	♂inf	♂juv	♂	♀inf	♀2	♀1

each evening. The observer left this site after dusk, and observations were initiated at the same site the following morning. Overnight observations were conducted periodically to determine if the animals left the sleeping tree during the night-time hours.

The MSE group was observed monthly from October 1987 to February 1988. This group was captured for the second phase of the project in mid-March 1988. The LM1 group was observed monthly from October 1987 to December 1988.

Focal animal sampling (Altmann, 1974) was employed during all observations, except for two periods which will be discussed later. A total of five major activity categories were observed. These categories were defined as follows:

Feeding, during which an animal was actively consuming foods; this time may have included some mastication if the animal continued to consume food items.

Resting included both sleeping and resting behavior.

Moving was used to indicate traveling from point to point. No attempt was made to separate traveling from changes in position. A change in position within a space twice the animal's body length was not recorded as a "move".

Other provided a broad category which included drinking, howling, scent marking, urination, defecation, play, nursing, and other extraneous activities.

NIV (not in view) was used when the animal had moved out of the field of vision of the observer or the activity could not be defined.

Feeding behavior was the primary activity of interest in this study. No attempt was made to distinguish between feeding and foraging time (searching for food) during most of the sampling period. During the feeding time, specific information was collected concerning the food item selected. The plant species consumed was recorded. If the plant was not identifiable, the individual plant consumed was tagged and numbered for later identification. The part of the plant selected was recorded, as was the phenologic stage of the plant part. The estimation of stage of growth included the following definitions:

Mature leaves included all of the leaf material which had reached the mature size and coloration characteristic of the plant.

Young leaves were those which had nearly reached

(~80% of mature) the characteristic size of the species but not the color. This was the stage prior to maturation.

New leaves were both smaller and lighter in color than the leaves characteristic of the mature plant. These were typically leaves which had recently erupted from the bud stage.

Leaf buds were those leaves which were still in the bud stage.

Flowers included the entire portion of the flower including the petals and sepals.

Flower buds were those flowers that had not yet opened.

Ripe fruits were those fruits which had reached maturity.

Unripe fruits included those fruits which had not yet reached maturity.

Fruit was a general term used when the maturity of the fruit was unknown or could not be identified.

Stem was used to define the woody portion of a plant, typically near the apex of the branch.

Bark included the cambium layer.

Petiole was the structural portion of the leaf that supports the blade of the foliage.

Pulvinus was that swollen portion of the petiole at which the leaf was attached to the stem or branch of the plant.

In addition to the plant part selected and the time spent feeding on a specific plant part, the numbers of bites taken of the plant part were recorded. In some cases, depending on the plant part (e.g., fruits, flowers), the numbers of individual parts consumed were indicated.

Play activity was defined as wrestling between individuals. Also, some solitary play was observed, typically by infants or juveniles interacting with plants. Animals were considered to be nursing if the female's nipple was in the infant's mouth. An example of the field notes collected during a sampling period is provided in Table 2-4.

Two series of overnight observations were conducted, one in each season, to determine if the howlers were active after dusk. The sampling period was initiated after dusk, at approximately 18:30, and was terminated at dawn, at approximately 06:30 the following day. These observations were integrated into the monthly observations, creating two periods during which the animals were under continuous observation for 36 hr. During the overnight observations, a scan sampling of the entire group was conducted every 10 min.

A digital wrist watch was used to time the duration of specific activities. The length of an activity was rounded to the nearest 0.5 min.

Plant Sample Collection and Analysis

Plant samples were collected monthly following the completion of behavioral observations. The species and plant parts collected were based upon the behavioral results of that mo, with emphasis placed upon obtaining samples of those plant parts comprising the top 90% of feeding time. If a

Table 2-4. Example of field notes used for recording behavioral observations of a focal animal in LM1 group.

Time	Activity	Plant species	Bites	Part
16:25	FEED	<i>Marsdenia undulata</i>	6	Leaf
16:26.30	REST			
16:27.30	MOVE			
16:28	FEED	<i>Pithecellobium tortum</i>	6	Fruit
16:29	MOVE			
16:29.30	FEED	<i>Pithecellobium tortum</i>	9	Fruit
16:30.30	MOVE			
16:31.30	FEED	<i>Pithecellobium tortum</i>	2	Leaf
16:32	FEED	<i>Marsdenia undulata</i>	3	Leaf
16:32.30	MOVE			
16:33	FEED	<i>Platymiscium diadelphum</i>	45	Leaf
16:39	MOVE			
16:40	FEED	<i>Pithecellobium tortum</i>	3	Leaf
16:40.30	REST			
16:41.30	MOVE			
16:42	FEED	<i>Marsdenia undulata</i>	4	Leaf
16:42.30	REST			
16:43	FEED	<i>Marsdenia undulata</i>	22	Leaf
16:46	MOVE			
16:47	FEED	<i>Marsdenia undulata</i>	5	Leaf
16:47.30	MOVE			
16:49.30	FEED	<i>Pithecellobium tortum</i>	6	Leaf
16:50.30	MOVE			
16:51	FEED	<i>Pithecellobium tortum</i>	65	Leaf
16:59.30	MOVE			

representative sample could not be obtained for that mo, then at least one sample for either season (wet, dry) was collected.

There are several sources of variability inherent in determination of food selection by behavioral observation. It is impossible to obtain the specific plant part consumed by the animals. This may introduce uncertainty as to how representative the collected plant parts were of the plant parts consumed. Although a part may remain on a plant, which then can be collected for analysis, that part may have been discriminated against by the animal for reasons not readily apparent to the person collecting the plant part. An additional concern was the impact of sample collection on the availability of foods for the study groups, and the effect this may have on the following month's observations. For this reason, the sample collection occurred after completion of the monthly behavioral observations, with approximately 3 wk to permit regrowth before the next observation period.

Every attempt was made to collect samples from the study site or, if not possible, the area immediately surrounding the two territories. A sample similar to the consumed portion of the plant was collected with a targeted minimum sample size of 200 g. Samples were sealed in plastic bags to prevent moisture loss and delivered to the field laboratory. Fresh samples were weighed and dried in a forced-air drying oven at

60°C until reaching a constant weight (i.e., same weight over three consecutive measurements). The dried samples were then placed in a plastic bag, sealed, and shipped to the Comparative Nutrition Laboratory at Michigan State University (East Lansing, MI) for analysis.

Dried samples were ground in a Wiley mill fitted with a 2-mm screen. Samples were analyzed for dry matter (DM), crude protein ($[N] \times 6.25$) (CP), ether extract (EE), ash, gross energy (GE), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), cellulose (C), acid-detergent lignin (ADL), Ca, P, Mg, Na, K, Fe, Cu, Mn, Se, Zn. All nutrients were determined using AOAC official methods (AOAC, 1990). Gross energy was determined by complete combustion of an approximately 1-g sample in a Parr adiabatic oxygen bomb calorimeter (Parr Instrument Co., Moline, IL). Fiber components (NDF, ADF, ADL, and C) were determined by using nonsequential detergent fiber fractionation as described by Goering and Van Soest (1970). An approximately 1-g subsample was used for the procedure. All proximate and fiber analyses were performed in duplicate, unless small sample size dictated otherwise.

Mineral concentrations were determined using dried samples digested with nitric-perchloric acid (Fenton and Fenton, 1979). Concentrated nitric acid (20.0 ml) and 70% perchloric acid (5.0 ml) were added to approximately 1 g of ground sample in a Phillip's beaker. The sample was digested

until 1 ml of acid remained in the beaker. Following digestion, the samples were diluted with ddH₂O. All samples were digested in duplicate. All mineral concentrations, except P and Se, were analyzed using an atomic absorption/emission spectrophotometer (Smith-Hieftje 4000, Thermo-Jarrell Ash). Phosphorus was measured by colorometric spectrophotometry. Selenium was determined using the sensitive fluorometric assay of Whetter and Ullrey (1978).

Mean weights were determined for selected parts of plant species consumed by red howlers. These individual weights were determined using part or all of the plant samples collected for nutrient analysis.

Intake Estimation

Six mos (March, 1988) after the initial field observations began, one of the study groups (MSE) was selected for transfer to holding facilities on the ranch for more intensive study. These animals were chemically immobilized with a dart gun using Telazol® (tiletamine/zolazepam) at a concentration of 200 mg/ml. A mean dose of 23.3 mg/kg was used, with a range from 13.0 mg/kg to 37.5 mg/kg (Crissey and Edwards, 1989). Immobilized animals were caught in a large blanket, as they fell from the trees, to prevent injury from impact with the ground. The juvenile male (σ juv) was the first individual immobilized. It was felt that this animal

was the most likely to flee when the capture procedure was initiated. The adult females were then immobilized. When the first female (♀2) was immobilized, her male offspring (♂inf) also fell, clinging to her. Recognizing this as the ideal method of capturing the infant animals, it was hoped that the second infant (♀inf) would also cling to her mother during immobilization. This, unfortunately, was not the case, as the female infant (♀inf) jumped free of her mother prior to her mother's fall into the blanket. This necessitated the immobilization of the female infant (♀inf), which was conducted without incident. The adult male (♂) was the final animal of the group to be immobilized and transferred to the holding facilities.

In addition to the animals in the MSE study group, 7 animals from 2 groups peripheral to the MSE home range were immobilized following the guidelines above. Anatomical data (e.g., body weight, linear measurements) was collected, the animals were fitted with ear tags, and then released.

The holding facilities were located near the principal living area at Hato Masaguaral, which was approximately 2 km from the study site. The holding facilities were designed specifically to house red howlers. The sides of the enclosure, chain link mesh, were all open to the surrounding environment, although a solid roof covered the entire structure. A perimeter fence (~2 m) surrounded the enclosure

to prohibit feral dogs and pigs from entering.

The enclosure was 7.8 m long x 5.75 m high x 4.08 m deep. The floor of the enclosure was 1.0 m above a concrete slab, allowing easy access to the floor beneath for cleaning. The floor was covered by metal pans that could be removed for cleaning or collection of samples without entry into the cage.

The total structure was divided into five sections, four of which were equal in size (1.3 m x 5.75 m x 4.08 m) with the fifth twice as wide as the other four (2.6 m x 5.75 m x 4.08 m). The sections were interconnected with shift doors located 3.05 m above the floor of the enclosure. Divisions between sections were made of the same wire mesh as the outer sides, allowing visual, olfactory, and vocal communication when the animals were physically separated.

The interior of each section was furnished with numerous tree limbs, branches, and ropes to provide climbing structures. At the front of each section was a wooden shelf (1.3 m x 0.5 m) located 3.05 m above the floor of the enclosure. A graduated container for drinking water was placed upon this shelf. Additionally, there was a hanging platform (0.75 m x 0.75 m) in the center of each section. The platform in the largest of the five sections had a spring scale attached to it, creating a means by which the animals could be regularly weighed.

The enclosure flooring and hanging platforms were cleaned

daily. The animals were group-fed three times daily. The first feeding consisted of a "higher" fiber primate diet.

Selected nutrient specifications of this extruded diet are provided in Table 2-5. The primate diet was placed in pans on the hanging platforms. This helped entice the animals to use the hanging platforms frequently and thus facilitated the weighing of individuals. The two remaining daily feedings were of fresh browse which was collected from the surrounding area immediately prior to feeding.

Table 2-5. Selected nutrient composition of a "higher" fiber primate diet^a fed to captive red howlers in Venezuela (dry matter basis).

Nutrient	Concentration (%)
Dry matter	92
Crude protein	25
Ether extract	4.9
Crude fiber	10.9
Acid-detergent fiber	14.7-17.4

^aMarion Zoological, Inc., Plymouth, MN.

Water consumption was monitored daily. A container of equal size and volume, placed in an area inaccessible to the howlers, also was monitored to determine daily evaporation rates. This correction factor was needed to accurately determine water intake by the animals. All water containers were replenished daily.

The adult animals in the group (one ♂, two ♀♀) were used

to determine the mean bite weight of specific food items selected by animals observed in the wild. A pre-weighed portion of each food item was offered to one of the adult animals which had been temporarily isolated from the remainder of the group. The number of bites taken from each portion were recorded, and the remaining portion of the sample was re-weighed. Concurrently, a representative sample of the same food item was weighed, handled in the same manner as the other samples, and re-weighed following the procedure. This sample was used as a control to correct for any desiccation that may have occurred during the procedure.

Daily intake of a nutritionally complete, "higher" fiber extruded primate diet by three (2♂♂, 1♀) of the howlers was measured for 9 d. Weighed quantities of the higher fiber primate diet were offered each morning. Orts were removed in the late afternoon (~18:00), weighed and discarded.

Nutrient Composition of Consumed Diet

By integrating data from the above three areas of study, estimates of the nutrient composition of the diet consumed by free-ranging red howlers were made. For example, a free-ranging, adult ♂ red howler was observed to take 131 bites of *Pithecellobium saman* leaves. The mean bite weight of leaves of that plant species was 0.4 g as determined with trials involving the captive, adult ♂ red howler. Therefore, the

consumed weight of 131 bites of *Pithecellobium saman* leaves was estimated to be 52.4 g (as fed basis). Selected nutrient analyses of *Pithecellobium saman* leaves indicated that the plant contained 38.3% dry matter and 5.61 kcal GE/g (DMB). Thus, within the 52.4 g of consumed leaf material, the animal had consumed 20.1 g of dry matter (32.3 g of moisture) and 112.8 kcal of GE.

Similar calculations were made from the annual behavioral observations for the three adult animals (1♂, 2♀♀) in LM1 to estimate nutrient composition of the consumed diet.

Results

Behavioral Observations

The behavioral data for the adult animals (1♂, 2♀♀) of group MSE consisted of 180 focal-animal h collected from October, 1987 through February, 1988. This data set was not divided according to season (dry versus wet). Time budgets within the 12-h dawn to dusk observation period are provided in Table 2-6.

The behavioral data for group LM1 consisted of 912 focal animal h. Adult animals (1♂, 2♀♀) of the group comprised 432 focal-animal h of that total time, collected during 12 consecutive mos from January 1988 through December 1988. The 1988 dry season data included observations from January through May (5 mos). Wet season data included

Table 2-6. Distribution (%) of daily activities of three adult (1♂, 2♀♀) red howlers (group MSE).

Activity	Time (%)	Time (hr)
Rest	76.6	9.2
Feed	13.1	1.6
Move	8.2	1.0
Other	1.5	0.2
NIV	0.6	0.1

observations made from June through November (6 mos). December 1988 was a transition mo between wet and dry season, and was not included in the results. The distribution of daily activities expressed on an annual, dry season, and wet season basis is provided in Table 2-7.

The distribution of time spent feeding (group MSE) on major plant parts (leaf, fruit, flower) is given in Figure 2-5. Consumption data, divided among more specific food plant parts, are shown in Figure 2-6.

Table 2-7. Distribution of daily activities of three adult (1♂, 2♀♀) red howlers (group LM1) expressed on an annual, dry season, and wet season basis.

Activity	Annual		Dry Season		Wet Season	
	min	%	min	%	min	%
Rest	543.0	75.4	540.7	75.1	542.9	75.4
Feed	90.7	12.6	88.6	12.3	96.5	13.4
Move	54.0	7.5	62.6	8.7	14.4	6.2
Other	28.8	4.0	24.5	3.4	31.7	4.4
NIV	3.6	0.5	2.9	0.4	4.3	0.6

Figure 2-5. Major plant parts (leaf, fruit, flower) consumed by red howlers (group MSE), listed as percent of observed feeding time.

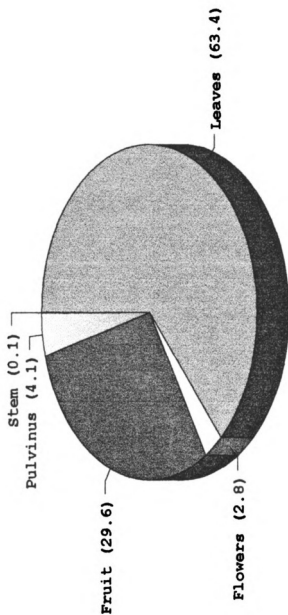
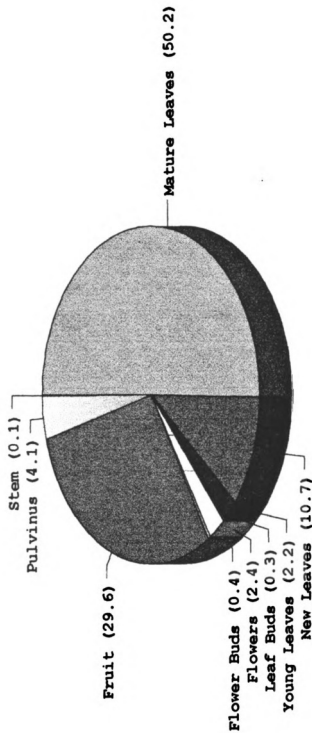


Figure 2-6. Specific plant parts consumed by red howlers (group MSE), listed as percent of observed feeding time.



The distribution of feeding time (group LM1) on general plant parts (leaf, fruit, flower) is presented in Figure 2-7 (annual), Figure 2-8 (dry season), and Figure 2-9 (wet season). The distribution of time spent feeding on plant parts, at specific stages of maturity (e.g., ripe, unripe), is presented in Figures 2-10, 2-11, 2-12.

Food plant species and parts consumed by group LM1, ranked by total annual feeding time, dry season feeding time, and wet season feeding time, are listed in Tables 2-8, 2-9, and 2-10, respectively.

Throughout the entire study, the howlers were never observed to consume animal-based foods. This does not exclude the possibility of secondary ingestion of insects which may be associated with food plants during some stage of their life-cycle.

The two 12-h dusk (18:00) to dawn (06:00) observation periods revealed that this group of red howlers was not active during that time period, with "resting" comprising 100% of the night time scan samples.

Plant Sample Collection and Analysis

A total of 171 individual plant samples was collected during the study period, representing parts from 36 species. Dry matter, crude protein, ether extract, ash, and fiber component (NDF, ADF, ADL, C) concentrations for these samples

Figure 2-7. Major plant parts (leaf, fruit, flower) consumed by red howlers (group LM1), listed as percent of total annual feeding time.

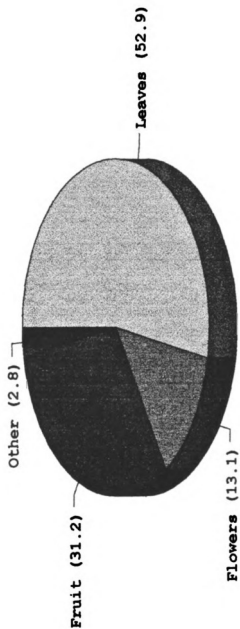


Figure 2-8. Major plant parts (leaf, fruit, flower) consumed by red howlers (group LM1), listed as percent of total dry season feeding time.

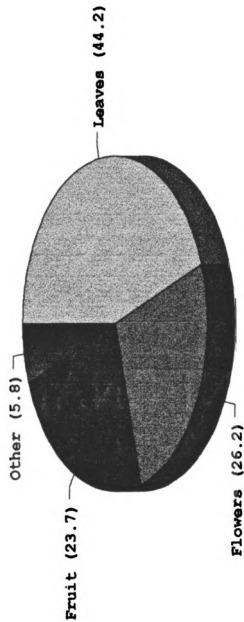


Figure 2-9. Major plant parts (leaf, fruit, flower) consumed by red howlers (group LM1), listed as percent of total wet season feeding time.

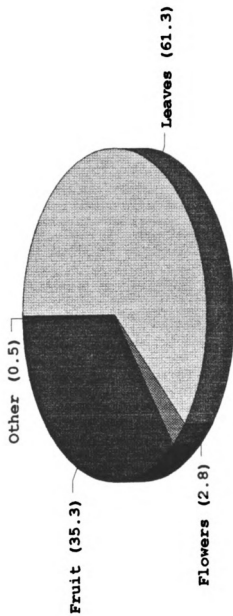


Figure 2-10. Specific plant parts consumed by red howlers (group LM1), listed as percent of total annual feeding time.

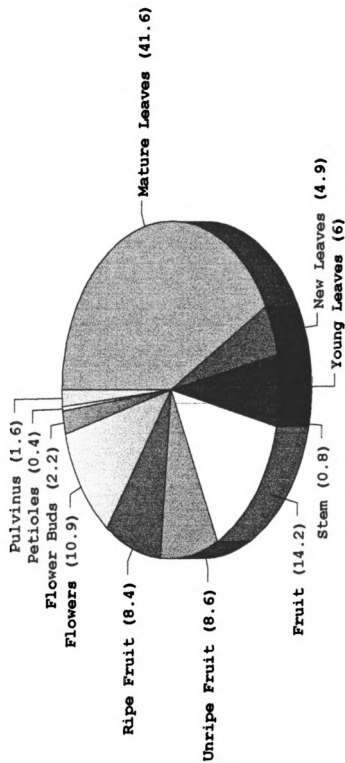


Figure 2-11. Specific plant parts consumed by red howlers (group LM1), listed as percent of total dry season feeding time.

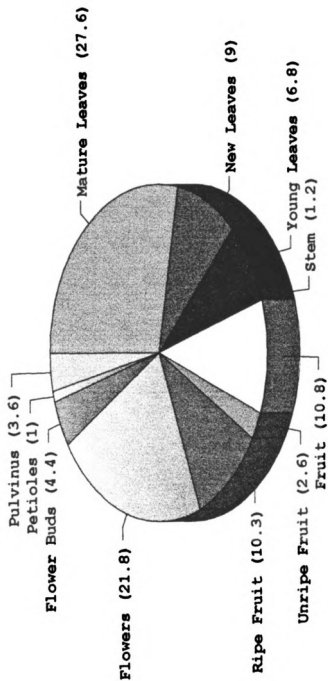


Figure 2-12. Specific plant parts consumed by red howlers (group IM1), listed as percent of total wet season feeding time.

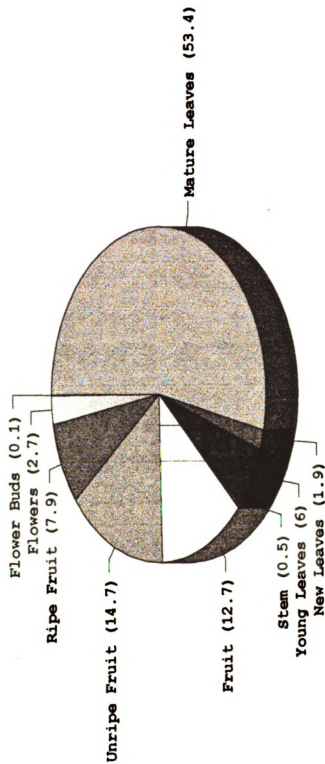


Table 2-8. Food plant species and part consumed by red howlers (group IM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
1	<i>Guazuma ulmifolia</i>	F	(81)	241.5	7.38
2	<i>Ficus pertusa</i>	UF	(64)	211.0	6.45
3	<i>Albizia guachapele</i>	L	(34)	188.0	5.75
4	<i>Pithecellobium saman</i>	FL	(46)	174.0	5.32
5	<i>Pithecellobium saman</i>	L	(41)	173.5	5.30
6	<i>Ficus pertusa</i>	L	(62)	161.5	4.94
7	<i>Guazuma ulmifolia</i>	FL	(84)	153.0	4.68
8	<i>Mangifera indica</i>	RF	(4)	148.5	4.54
9	<i>Pithecellobium tortum</i>	L	(49)	141.0	4.31
10	<i>Ficus pertusa</i>	RF	(65)	110.5	3.38
11	<i>Zizyphus saeri</i>	F	(70)	88.0	2.69
12	Unidentified #01	L	(74)	79.0	2.42
13	<i>Cassia grandis</i>	L	(26)	78.0	2.38
14	<i>Licania pyrifolia</i>	L	(22)	67.0	2.05
15	<i>Licania pyrifolia</i>	NL	(21)	65.0	1.99
16	<i>Sterculia apetala</i>	FLBU	(87)	63.0	1.93

Table 2-8 (cont'd). Food plant species and part consumed by red howlers (group IM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
17	<i>Entada sp.</i>	L	(54)	59.5	1.82
18	<i>Cassia moschata</i>	L	(28)	57.0	1.74
19	<i>Marsdenia undulata</i>	L	(16)	52.0	1.59
20	<i>Mangifera indica</i>	PUL	(5)	52.0	1.59
21	<i>Copernicia tectorum</i>	F	(12)	48.0	1.47
22	<i>Pterocarpus acapulcensis</i>	L	(60)	44.0	1.35
23	<i>Zanthoxylum culantrillo</i>	YL	(78)	38.5	1.18
24	<i>Zanthoxylum culantrillo</i>	L	(76)	37.0	1.13
25	<i>Pterocarpus acapulcensis</i>	NL	(61)	37.0	1.13
26	Unidentified #04	L	-	36.0	1.10
27	<i>Zizyphus saeri</i>	L	(68)	34.0	1.04
28	<i>Mangifera indica</i>	UF	(2)	33.5	1.02
29	Unidentified #02	YL	(90)	33.5	1.02
30	<i>Cassia moschata</i>	YL	(30)	32.5	0.99
31	<i>Cassia moschata</i>	UF	(32)	31.5	0.96
32 †	<i>Licania pyrifolia</i>	YL	(21)	25.5	0.78

Table 2-8 (cont'd). Food plant species and part consumed by red howlers (group LM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
33	<i>Pithecellobium dualense</i>	FL	(40)	25.5	0.78
34	Unidentified #03	L	(91)	25.5	0.78
35	<i>Sterculia apetala</i>	ST	-	21.5	0.78
36	<i>Perskia guamacho</i>	F	(19)	19.0	0.58
37	<i>Guazuma ulmifolia</i>	NL	-	18.0	0.55
38	<i>Pithecellobium saman</i>	YL	(44)	18.0	0.55
39	<i>Annona jahnii</i>	L	(6)	17.0	0.52
40	Unidentified #05	L	-	17.0	0.52
41	<i>Pithecellobium dualense</i>	L	(39)	16.5	0.50
42	<i>Annona puniceifolia</i>	RF	(11)	16.0	0.49
43	<i>Albizia guachapele</i>	YL	(36)	15.5	0.47
44	<i>Pithecellobium saman</i>	F	(47)	15.5	0.47
45	<i>Cassia grandis</i>	F	(27)	15.0	0.46
46	<i>Sapium aucuparium</i>	L	(25)	15.0	0.46
47	<i>Albizia guachapele</i>	NL	(37)	12.5	0.52
48	<i>Pithecellobium saman</i>	LBV	(43)	12.0	0.37
49	<i>Paullinia cururu</i>	L	(80)	11.5	0.35

Table 2-8 (cont'd). Food plant species and part consumed by red howlers (group LM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
50	<i>Pithecellobium tortum</i>	F	(53)	10.5	0.32
51	<i>Randia venezuelensis</i>	L	-	10.5	0.32
52	<i>Albizia columbiana</i>	L	(33)	10.0	0.31
53	<i>Pithecellobium saman</i>	PET	-	10.0	0.31
54	<i>Mangifera indica</i>	L	-	9.5	0.29
55	<i>Ceiba pentandra</i>	F	-	9.5	0.29
56	<i>Randia venezuelensis</i>	YL	(71)	9.5	0.29
57	<i>Sterculia apetala</i>	NL	-	8.0	0.24
58	Unidentified #06	F	-	8.0	0.24
59	<i>Pithecellobium tortum</i>	NL	(52)	7.5	0.23
60	<i>Mangifera indica</i>	NL	-	7.0	0.21
61	<i>Pithecellobium saman</i>	FLBU	(45)	6.5	0.20
62	<i>Ficus pertusa</i>	YL	-	6.5	0.20
63	<i>Pithecellobium saman</i>	NL	(43)	6.0	0.18
64	<i>Sterculia apetala</i>	FL	(86)	5.5	0.17
65	<i>Ceiba pentandra</i>	L	-	5.0	0.15
66	<i>Licania pyrifolia</i>	F	-	5.0	0.15

Table 2-8 (cont'd). Food plant species and part consumed by red howlers (group LM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
67	<i>Cassia grandis</i>	YL	-	5.0	0.15
68	<i>Guazuma ulmifolia</i>	L	-	5.0	0.15
69	<i>Annona jahnii</i>	UF	(7)	4.5	0.14
70	<i>Ceiba pentandra</i>	ST	-	4.5	0.14
71	<i>Ceiba pentandra</i>	PET	-	4.0	0.12
72	<i>Zizyphys saeri</i>	YL	-	4.0	0.12
73	<i>Ficus sp.</i>	L	-	3.5	0.11
74	<i>Melothria trilobata</i>	L	-	3.0	0.09
75	<i>Guazuma ulmifolia</i>	YL	-	3.0	0.09
76	Unidentified #07	L	-	3.0	0.09
77	<i>Coccoloba sp.</i>	YL	-	2.5	0.08
78	<i>Genipa americana</i>	F	-	2.0	0.06
79	Unidentified #08	FLBU	-	2.0	0.06
80	<i>Entada sp.</i>	YL	-	1.5	0.05
81	Unidentified #09	L	-	1.5	0.05
82	Unidentified #10	F	-	1.0	0.03
83	<i>Mangifera indica</i>	FLBU	-	0.5	0.02

Table 2-8 (cont'd). Food plant species and part consumed by red howlers (group IM1), ranked by total annual feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
84	<i>Marsdenia undulata</i>	F	(17)	0.5	0.02
85	<i>Tetracera volubris</i>	L	-	0.5	0.02

^aL=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus.

^bReference number corresponds to sample nutrient analysis provided in Appendix Tables A1-A21.

†Plant parts ranked from 1 through (†) represent 90.2% of total annual feeding time.

Table 2-9. Food plant species consumed by red howlers (group LM1), ranked by total dry season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
1	<i>Pithecellobium saman</i>	FL	(46)	174.0	12.03
2	<i>Mangifera indica</i>	RF	(4)	148.5	10.27
3	<i>Guazuma ulmifolia</i>	FL	(84)	135.5	9.37
4	<i>Guazuma ulmifolia</i>	F	(83)	116.5	8.05
5	<i>Albizia guachapele</i>	L	(35)	91.0	6.29
6	<i>Licania pyrifolia</i>	NL	(21)	65.0	4.49
7	<i>Pithecellobium saman</i>	L	(42)	64.5	4.46
8	<i>Licania pyrifolia</i>	L	(22)	62.0	4.29
9	<i>Sterculia apetala</i>	FLBU	(87)	57.0	3.94
10	<i>Mangifera indica</i>	PUL	(5)	52.0	3.59
11	<i>Cassia moschata</i>	L	(29)	42.0	2.90
12	<i>Zizyphus saeri</i>	L	(69)	34.0	2.35
13	<i>Cassia moschata</i>	YL	(31)	32.5	2.25
14	Unidentified #02	YL	(90)	29.0	2.00
15	<i>Licania pyrifolia</i>	YL	-	25.5	1.76
16	<i>Ficus pertusa</i>	L	(62)	21.5	1.49
17	<i>Mangifera indica</i>	UF	(2)	21.0	1.45

Table 2-9 (cont'd). Food plant species consumed by red howlers (group IM1), ranked by total dry season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
18	<i>Pterocarpus acapulcensis</i>	NL	(61)	19.5	1.35
19	<i>Sterculia apetala</i>	ST	(89)	18.0	1.24
20	<i>Cassia moschata</i>	UF	(32)	17.0	1.18
21	Unidentified #04	L	-	16.5	1.14
22	<i>Pithecellobium saman</i>	F	(48)	15.5	1.07
23	Unidentified #03	L	(91)	14.5	1.00
24	<i>Albizia guachapele</i>	NL	(37)	12.5	0.86
25	<i>Pithecellobium saman</i>	LBU	-	12.0	0.83
26†	Unidentified #05	L	-	12.0	0.83
27	<i>Cassia grandis</i>	L	-	11.5	0.80
28	<i>Guazuma ulmifolia</i>	NL	-	11.0	0.76
29	<i>Pithecellobium tortum</i>	F	(53)	10.5	0.73
30	<i>Pithecellobium saman</i>	PPT	-	10.0	0.69
31	<i>Mangifera indica</i>	L	-	9.5	0.66
32	<i>Ceiba pentandra</i>	F	-	9.5	0.66
33	<i>Annona Jahnnii</i>	L	(6)	8.5	0.59
34	<i>Sterculia apetala</i>	NL	-	8.0	0.55

Table 2-9 (cont'd). Food plant species consumed by red howlers (group IM1), ranked by total dry season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
35	<i>Pithecellobium tortum</i>	NL	(52)	7.5	0.52
36	<i>Pithecellobium tortum</i>	L	-	6.5	0.45
37	<i>Ficus pertusa</i>	YL	-	6.5	0.45
38	<i>Pithecellobium saman</i>	FLBU	(45)	6.5	0.45
39	<i>Pithecellobium saman</i>	NL	(43)	6.0	0.41
40	<i>Sterculia apetala</i>	FL	(86)	5.5	0.38
41	<i>Licania pyrifolia</i>	F	-	5.0	0.35
42	<i>Ceiba pentandra</i>	L	-	4.0	0.28
43	<i>Ceiba pentandra</i>	PET	-	4.0	0.28
44	<i>Zizyphus saeri</i>	YL	-	4.0	0.28
45	<i>Mangifera indica</i>	NL	-	1.0	0.07
46	<i>Sapium aucuparium</i>	L	-	1.0	0.07
47	<i>Coccoloba</i> sp.	YL	-	1.0	0.07
48	<i>Mangifera indica</i>	FLBU	-	0.5	0.03

^aL=young leaf; YL=young leaf; NL=new leaf; LBU=leaf bud; F=fruit; RF=ripe fruit; UF=unripe fruit; FL=flowers; FLBU=flower bud; PET=petiole; PUL=pulvinus; ST=stem.

^bReference number corresponds to sample nutrient analysis provided in Appendix Tables A1-A21.

†Plant parts ranked from 1 through (†) represent 90.5% of total dry season feeding time.

Table 2-10. Food plant species consumed by red howlers (group LM1), ranked by total wet season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
1	<i>Ficus pertusa</i>	UF	(64)	211.0	13.21
2	<i>Ficus pertusa</i>	L	(63)	140.0	8.77
3	<i>Ficus pertusa</i>	RF	(65)	110.5	6.92
4	<i>Pithecellobium saman</i>	L	(41)	96.5	6.04
5	<i>Albizia guachapele</i>	L	(34)	93.5	5.85
6	<i>Pithecellobium tortum</i>	L	(49)	92.0	5.76
7	<i>Zizyphs saeri</i>	F	(70)	88.0	5.51
8	<i>Entada</i> sp.	L	(54)	59.5	3.73
9	Unidentified #01	L	(74)	54.0	3.38
10	<i>Cassia grandis</i>	L	(26)	53.5	3.35
11	<i>Marsdenia undulata</i>	L	(16)	52.0	3.26
12	<i>Copernicia tectorum</i>	F	(12)	48.0	3.01
13	<i>Pterocarpus acapulcensis</i>	L	(60)	44.0	2.76
14	<i>Zanthoxylum culantrillo</i>	YL	(78)	38.5	2.41
15	<i>Zanthoxylum culantrillo</i>	L	(76)	37.0	2.32
16	<i>Pithecellobium dualense</i>	FL	(40)	25.5	1.60
17	<i>Guazuma ulmifolia</i>	F	(81)	21.0	1.31

Table 2-10 (cont'd). Food plant species consumed by red howlers (group LM1), ranked by total wet season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
18	<i>Pereskia guamacho</i>	F	(19)	19.0	1.19
19	Unidentified #04	L	-	19.0	1.19
21	<i>Guazuma ulmifolia</i>	FL	(85)	17.5	1.10
22	<i>Pterocarpus acapulcensis</i>	NL	(61)	17.5	1.10
23	<i>Pithecellobium dualense</i>	L	(39)	16.5	1.03
24	<i>Annona punicifolia</i>	RF	(11)	16.0	1.00
25	<i>Albizia guachapele</i>	YL	(36)	15.5	0.97
26	<i>Cassia grandis</i>	F	(27)	15.0	0.94
27	<i>Sapium aucuparium</i>	L	(25)	14.0	0.88
28	<i>Mangifera indica</i>	UF	(3)	12.5	0.78
29†	<i>Faullinia cururu</i>	L	(80)	11.5	0.72
30	Unidentified #03	L	(91)	11.0	0.69
31	<i>Randia venezuelensis</i>	L	-	10.5	0.66
32	<i>Albizia columbiana</i>	L	(33)	10.0	0.63
33	<i>Randia venezuelensis</i>	YL	(71)	9.5	0.59
34	<i>Annona jahnnii</i>	L	(6)	8.5	0.53
35	<i>Cassia moschata</i>	L	(28)	8.0	0.50

Table 2-10 (cont'd). Food plant species consumed by red howlers (group IM1), ranked by total wet season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
36	Unidentified #06				
37	<i>Guazuma ulmifolia</i>	L	-	8.0	0.50
38	<i>Cassia moschata</i>	NL	-	7.0	0.44
39	<i>Mangifera indica</i>	UF	(32)	6.5	0.41
30	<i>Cassia grandis</i>	NL	-	6.0	0.38
41	<i>Guazuma ulmifolia</i>	YL	-	5.0	0.31
42	<i>Annona jahnii</i>	L	-	5.0	0.31
43	<i>Ceiba pentandra</i>	UF	(7)	4.5	0.28
44	Unidentified #02	ST	-	4.5	0.28
45	<i>Ficus sp.</i>	YL	-	4.5	0.28
46	<i>Sterculia apetala</i>	L	-	3.5	0.22
47	<i>Melothria trilobata</i>	ST	(89)	3.5	0.22
48	<i>Guazuma ulmifolia</i>	L	(23)	3.0	0.19
49	Unidentified #07	YL	-	3.0	0.19
50	<i>Genipa americana</i>	L	-	3.0	0.19
51	Unidentified #08	F	-	2.0	0.13
		FLBU	-	2.0	0.13
52	<i>Entada sp.</i>	YL	-	1.5	0.09

Table 2-10 (cont'd). Food plant species consumed by red howlers (group IM1), ranked by total wet season feeding time.

Rank	Plant species	Part ^a	Species no. ^b	Feeding time (min)	Feeding time (% of total)
53	Unidentified #09	L	-	1.5	0.09
54	<i>Ceiba pentandra</i>	L	-	1.0	0.06
55	<i>Coccoloba</i> sp.	YL	-	1.0	0.06
56	Unidentified #10	F	-	1.0	0.06
57	<i>Tetracera volubris</i>	L	-	0.5	0.03

^aL=mature leaf; YL=young leaf; NL=new leaf; LBU=leaf bud; F=fruit; RF=ripe fruit; UF=unripe fruit; FL=flower; FLBU=flower bud; PET=petiole; PUL=pulvinus; STEM=stem.

^bReference number corresponds to sample nutrient analysis provided in Appendix Tables A1-A21.

†Plant parts ranked from 1 through (†) represent 90.2% of total wet season feeding time.

are provided in Appendix Tables A1-A7. Macro-mineral (Ca, P, Na, K, Mg) concentrations are given in Appendix Tables A8-A14. Trace element (Fe, Cu, Mn, Se, Zn) concentrations are given in Appendix Tables A15-A21.

Average weights of specific plant parts, which were used to supplement the bite weight data (see below), are provided in Table 2-11.

Intake Estimation

The average bite weights of an adult male (σ) and two adult females ($\text{♀}1$, $\text{♀}2$) were determined for parts of some of the plants. The plants were those upon which 90% of the feeding time of free-ranging animals was spent, determined by the field observations. Table 2-12 provides the average bite weight for the specific plant parts tested.

The mean body weights of free-ranging red howlers, collected during immobilization procedures, are provided in Table 2-13. Levels of daily consumption of the higher fiber primate diet by three of the captive animals during a 9-d trial are given in Table 2-14.

Nutrient Composition of Consumed Diet

Integrating information from the results of the three areas of study, daily food intake by free-ranging howlers was calculated to be 544.0 g, on an as-fed basis, or 151.0 g of

Table 2-11. Average fresh weight of plant parts consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	n	Weight (g)	
				Mean	SD
Anacardiaceae					
<i>Mangifera indica</i>	(2, 3)	UF ^b	28	135.24	19.446
<i>Mangifera indica</i>	(4)	RF	54	139.13	29.619
<i>Mangifera indica</i>	(5)	PUL	280	0.13	0.036
Annonaceae					
<i>Annona jahni</i>	(6)	L	100	1.11	0.306
<i>Annona jahni</i>	(7)	UF	7	10.90	-
<i>Annona jahni</i>	(8)	RF	11	69.50	
<i>Annona puniceifolia</i>	(10)	UF	14	24.90	-
<i>Annona puniceifolia</i>	(11)	RF	41	49.64	6.336
Arecaceae					
<i>Copernicia tectorum</i>	(15)	RF	33	6.22	0.790
Asclepidaceae					
<i>Marsdenia undulata</i>	(16)	L	63	0.88	0.455
<i>Marsdenia undulata</i>	(17)	UF	20	127.87	18.020
Cactaceae					
<i>Pereskia guamacho</i>	(19)	RF	18	3.94	0.918

Table 2-11 (cont'd). Average fresh weight of plant parts consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	n	Weight (g)	
				Mean	SD
Dilleniaceae					
<i>Tetracera volubris</i>	(24)	FL	15	0.04	0.074
Euphorbiaceae					
<i>Sapium aucuparium</i>	(25)	L	94	0.51	0.218
Fabaceae (Caesalpinioideae)					
<i>Cassia grandis</i>	(26)	Llft	108	0.62	0.050
Fabaceae (Mimosoideae)					
<i>Pithecellobium saman</i>	(43)	NL	100	0.87	0.550
<i>Pithecellobium saman</i>	(44)	YL	57	3.53	1.229
<i>Pithecellobium saman</i>	(48)	UF	7	19.34	10.057
<i>Pithecellobium tortum</i>	(49)	Lflt	54	0.44	0.197
<i>Pithecellobium tortum</i>	(53)	UF	50	1.79	0.872
Fabaceae (Papilionoideae)					
<i>Platymiscium diadelphum</i>	(56)	Lflt	100	0.42	0.186
Rubiaceae					
<i>Randia venezuelensis</i>	(73)	UF	64	1.10	0.224
Rutaceae					
<i>Zanthoxylum culantrillo</i>	(76)	Lflt	54	0.47	-

Table 2-11 (cont'd). Average fresh weight of plant parts consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	n	Weight (g)	
				Mean	SD
Sterculiaceae					
Sterculia apetala					
(86)		FL	80	0.26	0.074

^a L=mature leaf; Lfl=leaflet; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

^b All fruit weights include seeds unless otherwise indicated.

Table 2-12. Mean bite weight (g) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ species	Species no.	Part*	♂	n	♀1	n	♀2	n
Anacardiaceae								
<i>Mangifera indica</i>	(1)	YL	0.47	7	0.78	4	-	-
<i>Mangifera indica</i>	(2), (3)	UF	2.19	20	2.03	10	1.81	11
<i>Mangifera indica</i>	4	RF	2.39	11	1.82	22	1.96	21
Annonaceae								
<i>Annona puniceifolia</i>	(11)	RF	6.41	11	4.09	10	7.37	11
Arecaeae								
<i>Copernicia tectorum</i>	(15)	RF	0.87	9	1.07	10	1.09	10
Asclepidaceae								
<i>Marsdenia undulata</i>	(16)	L	0.89	10	0.55	11	0.82	10
<i>Marsdenia undulata</i>	(17)	UF	1.20	2	1.49	4	1.33	6
Cactaceae								
<i>Pereskia guamacho</i>	(19)	RF	-	-	4.18	11	3.40	5
Chrysobalanaceae								
<i>Licania pyrifolia</i>	(21)	NL	0.64	11	0.46	10	0.32	10
<i>Licania pyrifolia</i>	(22)	L	0.34	10	0.35	17	0.29	10
Dilleniaceae								
<i>Tetracera volubris</i>	(24)	FL	0.29	9	0.32	11	0.23	9

Table 2-12 (cont'd). Mean bite weight (g) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ species	Species no.	Part*	♂	n	♀1	n	♀2	n
Fabaceae (Caesalpinioideae)								
<i>Cassia grandis</i>	(26)	L	0.39	4	0.33	10	0.33	8
<i>Cassia moschata</i>	(28)	L	0.39	2	0.33	13	0.22	5
<i>Cassia moschata</i>	(32)	UF	-	-	1.32	3	1.64	1
Fabaceae (Mimosoideae)								
<i>Albizia guachapele</i>	(34, 35)	L	0.55	12	0.49	12	0.36	10
<i>Albizia guachapele</i>	(36)	YL	0.57	9	0.37	9	0.41	10
<i>Pithecellobium dualense</i>	(39)	L	0.39	1	-	-	-	-
<i>Pithecellobium dualense</i>	(40)	FL/BU	0.35	6	0.15	8	-	-
<i>Pithecellobium saman</i>	(41)	L	0.40	10	0.32	11	0.27	10
<i>Pithecellobium saman</i>	(45)	FLBU	0.93	14	0.81	12	0.67	12
<i>Pithecellobium saman</i>	(46)	FL	0.83	14	0.81	12	0.67	12
<i>Pithecellobium tortum</i>	(49)	L	0.39	11	0.28	12	0.17	13
<i>Pithecellobium tortum</i>	(52)	BU,NL	-	-	0.18	4	-	-
Fabaceae (Papilionoideae)								
<i>Entada polystachya</i>	(54)	L	0.46	7	0.40	12	0.27	4
<i>Pterocarpus acapulensis</i>	(60)	L	0.58	2	0.51	2	-	-
<i>Pterocarpus acapulensis</i>	(61)	NL	0.65	15	0.56	10	0.60	15

Table 2-12 (cont'd). Mean bite weight (g) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ species	Species no.	Part*	♂	n	♀1	n	♀2	n
Moraceae								
<i>Ficus pertusa</i>	(62)	L	0.45	10	0.37	10	0.43	10
<i>Ficus pertusa</i>	(64)	UF	0.24	11	0.26	10	0.24	10
<i>Ficus pertusa</i>	(65)	RF	0.27	10	0.30	10	0.34	5
Rubiaceae								
Unidentified #01	(75)	YL	0.31	12	0.16	11	0.36	10
Rutaceae								
<i>Zanthoxylum culantrillo</i>	(78)	YL	0.40	10	0.34	13	0.30	12
Sapindaceae								
<i>Paullinia cururu</i>	(78)	YL	0.35	10	0.22	10	0.24	10
Sterculiaceae								
<i>Guazuma ulmifolia</i>	(81)	F	1.03	10	0.67	11	1.02	10
<i>Guazuma ulmifolia</i>	(84)	FL	0.44	14	0.19	12	0.11	6
<i>Sterculia apetala</i>	(87)	FLBU	0.40	10	0.27	10	0.23	10
UNIDENTIFIED PLANTS								
Unidentified #02	(90)	L	0.30	8	0.22	7	0.29	14

* Lemnate leaf; NU=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table 2-13. Mean body weight of free-ranging red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Age Class/Sex	n	Mean BW (kg) $\pm$ SD
Adult $\sigma\sigma$	4	6.28 $\pm$ 0.90
Adult ♀♀	4	4.10 $\pm$ 0.37

Table 2-14. Body weight and daily feed intake of nutritionally complete, "higher" fiber primate diet^a by captive red howlers (*Alouatta seniculus*).

Animal	BW (kg)	Intake (g/d) (AFB)	Intake (g/d) (DMB)	Intake (% BW) (DMB)
Adult σ	6.58	146.1	134.4	2.04
Juvenile σ	4.31	101.5	93.4	2.17
Juvenile ♀	ND ^b	100.7	92.6	-

^aMarion Zoological, Inc., Plymouth, MN.

^bNot determined.

dry matter. Dry matter intake, as a percentage of mean body weight, was calculated as 3.13%. Mean gross energy intake was estimated to be 711.2 kcal/d. The calculated concentrations of proximate and fiber components in the diet of free-ranging animals are provided in Table 2-15. The calculated macro and trace mineral concentrations are given in Table 2-16. Estimates of dietary nutrient composition based alone on distribution of time feeding on specific plant parts are presented in Tables 2-17 and 2-18 for proximate and mineral concentrations, respectively.

The distribution of feeding among general plant parts (leaf, fruit, flower) based upon calculated mass intake is

Table 2-15. Calculated proximate and fiber composition of the mean annual diet selected by three adult (1♂, 2♀♀) red howlers (group LM1).

Nutrient	Concentration (DMB)
Dry matter (%)	27.8
Crude protein (%)	13.4
Crude fat (ether extract) (%)	3.6
Ash (%)	6.3
Gross energy (kcal/g)	4.71
Neutral-detergent fiber (%)	51.5
Acid-detergent fiber (%)	37.8
Acid-detergent lignin (%)	18.3
Cellulose (%)	19.0

Table 2-16. Calculated macro- and trace-mineral composition of the mean annual diet selected by three adult (1♂, 2♀♀) red howlers (group LM1).

Nutrient	Concentration (DMB)
Calcium (%)	0.78
Phosphorus (%)	0.19
Sodium (ppm)	97.3
Potassium (%)	1.6
Magnesium (%)	0.35
Iron (ppm)	126.8
Copper (ppm)	11.6
Manganese (ppm)	100.6
Selenium (ppm)	1.04
Zinc (ppm)	19.5

Table 2-17. Proximate nutrient composition (dry basis) of total diet as consumed by red howlers (group IM1) in the central llanos region of Venezuela calculated based on time spent feeding.

Nutrient	Annual	Wet Season	Dry Season
Dry matter (%)	27.1	29.4	27.3
Crude protein (%)	11.7	12.7	11.3
Ether extract (%)	2.7	3.2	2.2
Ash (%)	5.5	5.7	4.6
Gross energy (kcal/g)	4.18	4.30	3.91
Neutral-detergent fiber (%)	47.6	49.1	44.6
Acid-detergent fiber (%)	33.5	17.4	29.7
Acid-detergent lignin (%)	16.1	17.6	13.4
Cellulose (%)	16.7	18.0	15.6

Table 2-18. Macro and trace mineral composition (dry basis) of total diet as consumed by red howlers (group LMI) in the central llanos region of Venezuela calculated based on time spent feeding.

Nutrient	Annual	Wet Season	Dry Season
Calcium (%)	0.89	0.96	0.60
Phosphorus (%)	0.15	0.14	0.19
Calcium:Phosphorus	5.93	6.86	3.16
Sodium (ppm)	93.3	115.7	87.2
Potassium (%)	1.4	2.1	1.7
Magnesium (%)	0.38	0.49	0.25
Iron (ppm)	105.1	52.6	105.2
Copper (ppm)	9.7	9.9	10.1
Manganese (ppm)	91.6	122.5	59.4
Selenium (ppm)	2.39	4.39	0.18
Zinc (ppm)	17.1	17.2	18.0

presented in Figure 2-13. The distribution of calculated mass intake of plant parts, at specific stages of maturity (e.g., ripe, unripe), is presented in Figure 2-14.

Discussion

Behavioral Observations

The distribution of daily activities for adult howlers in both groups MSE and LM1 is comparable to that previously reported for both red howlers and other members of the genus *Alouatta*. Gaulin and Gaulin (1982) indicated that red howlers (*Alouatta seniculus*) in Andean cloud forest spent 78.5% of their time resting, 12.7% feeding, and 5.6% moving. Mantled howlers (*A. palliata*) in Costa Rica spent 72.5% of the observation time resting, 18.1% feeding, and 7.8% moving (Glander and Teaford, 1995). Milton (1978a) reported that mantled howlers on Barro Colorado rested 66.2%, and fed 15.6% of sample days.

The distribution of time spent feeding on general and specific plant parts was markedly different between the seasons. For the 12-mo study period, group LM1 spent over 50% of their feeding time consuming leaf material. Results from the 5-mo observations of group MSE were very similar to those of the main study group (LM1). Similarities are most likely due to the inclusion of animals in the same age/sex classes. Perhaps even more important are the similarities

Figure 2-13. Major plant parts (leaf, fruit, flower) consumed by red howlers (group IM1), listed as percent of calculated mass intake.

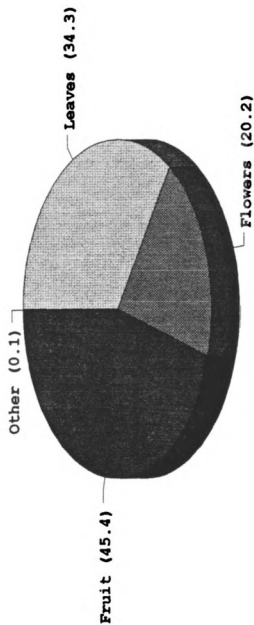
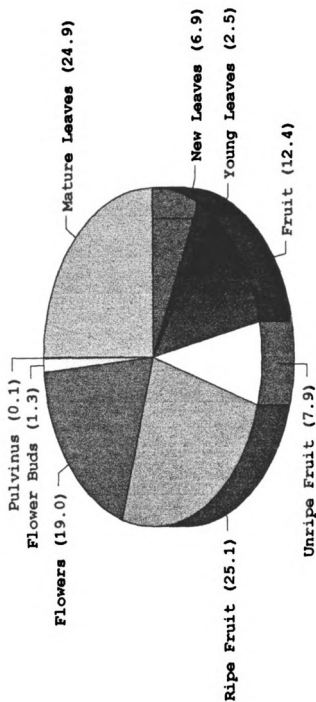


Figure 2-14. Specific plant parts consumed by red howlers (group LM1), listed as percent of calculated mass intake.



in habitat and vegetation between the two home ranges.

Although seasonal fluctuations were seen in the foods selected during the observations, these variations in plant part consumption appear to be more a function of phenology than preferential selection. Similar variation was reported in red howler consumption of fruits by Braza et al. (1983).

Regardless of how the feeding time was analyzed (seasonally, or general versus specific plant parts), mature leaf material was consistently the largest component of the diet (27.8%-53.5%). This is supported by observations of the brown howler (*A. fusca clamitans*) that spent 80% of feeding time consuming leaf material, 10% flowers, and 10% fruits (Galetti, et al., 1987). These foods were selected from more than 30 different species of plants. In contrast, red howlers in French Guiana selected from 195 plant species as food sources. The major food categories included young leaves (54%), mature fruits (21.5%) and flowers (12.6%). The remainder consisted of immature fruits (4%), mature leaves (3%), termitaria (1.5%), and bark (0.4%), respectively.

Major food categories selected by mantled howlers on Barro Colorado Island, Panama included leaves (43.5%), fruit (46.5%), and flowers (10%). Although these findings seem to coincide with the results presented here for red howlers, the conclusions provided by Milton (1978a) describe howlers as "behavioral folivores". This suggests that the animals seek

"less fibrous" and more digestible plant materials, due to their apparent lack of gastrointestinal modifications for fermentive digestion of plant cell wall. Although the time spent feeding on young leaves, fruits and flowers may increase, as they become seasonally available, it is apparent from the nutrient analyses presented below, as well as the quantified digestive capabilities of howlers (see Chapter III), many species within the genus *Alouatta* are quite capable "anatomical folivores".

A similar selective feeding pattern was also observed in both red colobus (*Colobus badius tephrosceles*) and black-and-white colobus (*Colobus guereza occidentalis*) (Baranga, 1982), both of which have been previously defined as "anatomical folivores". When available, these colobine primates demonstrated preferences for young plant growth of two species, which were both lower in fiber components and higher in crude protein, than the mature plants of the same plants.

When feeding time devoted to the plant part of an individual species was examined, the prominence of seasonally available food items became more apparent. During the dry season, over 40% of the time spent feeding focused on the flowers of *Pithecellobium saman* and *Guazuma ulmifolia* and the fruits of *Mangifera indica* and *Guazuma ulmifolia*. More than 20% of the wet season feeding time was involved in the consumption of ripe and unripe fruits of *Ficus pertusa*.

When expressed as a percent of the calculated mass intake, the quantities of consumed fruits (45.4%) are greater than either leaves (34.3%) or flowers (20.2%). This "shift" in distribution of selected foods is mostly likely due the amount of processing time involved when the animals are consuming leaves versus fruits. Additionally, the quantity of food harvested per individual bite, as measure with the captive individuals, was greater when comparing fruits, across species and animal sex (1.86 g/bite) to leaves (0.40 g/bite). Therefore, per unit of time, a red howler could ingest more fruit than leaves, by weight. This is the major limitation of making assessments of distribution of food plants among specific parts or nutrient content of the diet, based on time feeding alone.

The reliance on leaves provides the howler with a food source which presents essentially the same relative composition throughout the year (Rosenberger, 1992). The inclusion of fluctuating food resources reported in several species of howlers, within a single species, and even within a single group over a 12-mo period, indicates the adaptability of the genus. These variable feeding habits, which conform to seasonal fluctuations of plant phenology, are suggestive of an "intermediate feeder", a description proposed by Hoffman (1973), for ungulate herbivores with similar dietary habits.

Plant Sample Collection and Analysis

Nutrient analyses of plant materials provided a new level of insight as to the composition of natural foods selected by a free-ranging primate.

Suggestions that wild fruits, flowers, or immature leaves are consistently lower in plant cell wall and higher in readily fermentable carbohydrates constitute a very broad and over-simplified generalization. Much of this misconception is based on an image of "fruits" as the commercially propagated items purchased in a grocery store for human consumption. These cultivated foods are substantially different in nutrient composition from those wild foods analyzed. The hazards of the above generalization become even more apparent when one examines the dietary ingredients offered to many captive folivores and observes the unfortunate results of using inappropriate foods (see Chapter III).

Intake Estimation

Calculated estimates, using bite count and bite weight data, of dry matter intake by an adult, free-ranging red howler (151.0 g/d) were similar to measured intakes determined with the temporarily captive adult red howlers (134.4 g/d), as well as long-term (6 mo+) dry matter intakes determined with captive adult red howlers (134.0 g/d) (see Chapter III).

Gaulin and Gaulin (1982) estimated the dry matter intake

of red howlers living in the Andean cloud forest. Their method relied upon the average weight of individual plant parts and the number of items consumed per feeding bout. Although their reports of time spent feeding (12.7%) are nearly identical to those reported here (12.6%), their estimates of dry matter intake were nearly double (266 g/d) these calculated estimates. Dry matter intake of mantled howlers was estimated by Nagy and Milton (1979). Their estimates were based upon an indirect method combining energy expenditure assessments with measurements of caloric content of food items, feces, and urine. These results combined with the assumption that the mantled howlers' fresh food consisted of two-thirds water, were the basis for estimates of dry matter intakes of 348 g/d.

Estimates of fresh food intake by mantled howlers, using similar methods combining focal-animal sampling with collections of representative food items, were made by Hladik and Hladik (1969). They calculated that a typical mantled howler consumed 1.145 and 1.220 kg/d of fresh food in the mid and late wet seasons, respectively. Nagy and Milton (1979) estimated that a mantled howler required approximately 1 kg of fresh food/d. Gaulin and Gaulin's (1983) estimated a red howler's fresh food intake was 1.23 kg/d. Each study reported fresh food intakes greater than those reported here (544.0 g/d).

Dry matter intake is a more reliable estimate when making comparisons between studies, as it removes the variable effects of water. Unfortunately, dry matter intake was not determined by Hladik and Hladik (1969). Differences in plants selected and the nutrient composition of those plants, environmental and climatic stresses, and animal body mass all play a role in the regulation of food intake. These variables would certainly explain the differences seen between the estimate made in this study and the results of the captive feeding trials. However, it is difficult to conceive of conditions which could produce a nearly two-fold increase in dry matter intake within individuals of the same species.

These consistently inflated estimates of food intake may partially explain why previous researchers have suggested that howlers have relatively poor digestive capabilities. Herbivores lacking gastrointestinal adaptations that promote microbial fermentation of plant material typically exhibit a feeding strategy involving consumption of large quantities of food, rapid rates of passage, and short periods of retention. These adaptations allow the animal to process larger quantities of material per unit of time. None of these traits, characteristic of herbivores like the red panda (*Ailurus fulgens*) and ruffed lemur (*Varecia variegata*), are seen in howlers (see Chapter III).

Nutrient Composition of Consumed Diet

Estimates of dry matter composition and nutrient intake, based only on time spent feeding, were consistently lower than estimated composition of the diet based upon bite count and weight data. Further discussion concerning nutrient intake is based upon the bite count/weight estimates.

Moisture content of the red howlers' diet (72.2%) was slightly lower than that predicted by Gaulin and Gaulin (78%) (1982). A higher moisture content might be predicted in vegetation found in the Andean cloud forest, which is subjected to less dramatic changes in total annual rainfall, as compared to the Venezuelan llanos. The 5.8% difference in moisture concentrations is not sufficient, on its own, to explain the difference in results observed between these two studies.

Estimated crude protein (CP) concentration (13.4%) of the consumed diet was lower than NRC (1978) recommendations for captive primate diets, including both Old (15% CP) and New World ($\leq 25\%$ CP) Primates. The higher estimates of dietary protein need by New World Primates may apply more appropriately to the smaller sized tamarins and marmosets (Ofstedal, 1991).

Previous estimates of protein concentrations in diets consumed by wild red howlers, one made by Gaulin and Gaulin (1982), used a method combining bite counts per plant part and

average plant part weight previously described. These authors predicted a protein content of 5%. Hladik (1978) estimated the average crude protein content in the annual diet as 9.6%.

The dietary nutrient concentrations which were the most remarkable included the components of the plant cell wall, cellulose, hemicellulose, and lignin. These fiber fractions, measured as neutral-detergent fiber (NDF), acid-detergent fiber (ADF), and acid-detergent lignin were greater than anticipated, especially in view of earlier suggestions that howlers were unable to utilize fibrous foods. The calculated concentrations (51.5% NDF, 37.8% ADF, 18.3% ADL) in the diet selected by the red howlers were comparable to concentrations found in orchardgrass hay (55.1% NDF, 30.7% ADF) or timothy hay (64.2% NDF, 37.5% ADF) (NRC, 1989).

The earlier estimates of low concentrations of these complex carbohydrates and polymers in the wild diet may have provided the basis for the previous inferences that howlers are limited folivores compared with the Old World colobines. Obviously, the presence of high concentrations of plant fiber in the diet selected by red howlers in the llanos, suggests otherwise. Evidence supporting the red howlers' adaptations to folivory also is seen in modifications of the gastrointestinal tract (Table 2-19). Elongation of the large intestine and cecum create regions of reduced digesta flow, allowing populations of symbiotic microorganism to flourish.

The mechanism by which these organisms degrade plant cell wall and the benefits to the host have been described in detail elsewhere in this text.

The presence of lignin, a nearly indigestible compound that functions to protect plant materials from consumption by herbivores, was higher than would be predicted based on

Table 2-19. Length of different portions of the gastrointestinal tract of red howlers (mm) (Braza et al., 1983).

Component	♂♂ (n = 27)	♀♀ (n = 22)
Stomach (cardia-pylorus)	152.2 ± 29.3	145.5 ± 24.7
Stomach (pylorus-fundus)	188.6 ± 43.6	185.1 ± 37.6
Small intestine	2426.9 ± 166.7	2285.5 ± 205.8
Large intestine	1287.0 ± 247.4	1198.0 ± 181.1
Cecum	107.1 ± 7.8	101.8 ± 7.1

previous descriptions of howlers as "behavioral folivores". The relatively high ADL content (18.3%) of the selected diet was in excess of quantities recommended in captive animal diets, but still lower than those which promoted the formation of obstructive phytobezoars in folivorous primates fed highly lignified (23.6%) plant materials (Ensley et al., 1982). It should be noted that the formation of these phytobezoars has been reported primarily in colobine primates, although primates with a relatively less complex digestive system have also been affected (McClure et al., 1978).

Another variable which could explain of the measured ADL concentrations include the effects of tannins. Tannins will often confound the crude lignin analysis (Oftedal, 1991). Sequential analysis of the detergent fiber fractions will help to resolve contamination of the ADL by tannins.

The estimated macro mineral (calcium, phosphorus, potassium, magnesium, sodium) concentrations in the selected diet were typical for many range plant materials. All macro minerals, except sodium (see below) were consumed in quantities which met or exceeded the estimated nutrient requirements for primates (NRC, 1978).

Phosphorus concentrations (0.18%) were in the lower range of the NRC (1978) guidelines (0.2%). Marginal to deficient phosphorus concentrations in vegetation under range conditions have been commonly noted (Preston, 1977). The first reports of phosphorus deficiency in ungulates involved pica in animals in South Africa. These herbivores subsequently died from botulism as a result of consuming bones from rotted carcasses (Van Soest, 1982).

The concerns over marginal phosphorus concentrations are compounded when one considers the ratio of phosphorus which is available to the animal. A less available form of phosphorus bound by phytate, a hexaphosphoric acid ester of inositol, is commonly found in plant materials. Phytate also binds calcium and zinc producing less available forms. No measurements were

made to determine the extent of phytate binding of minerals in this study. However, phytate phosphorus may be partially available to the red howlers. As seen in other hindgut fermenters (Hintz et al., 1973), red howlers may possess some phytase activity produced by the microbial populations of the cecum and large intestine. Approximately 50% of phytate phosphorus is absorbed in animals and man that lack extensive microbial fermentation (Parfitt et al., 1964; NRC, 1989).

Estimates of dietary sodium concentrations (97.3 ppm DMB) were surprisingly low, when compared to both recommended dietary allowances for humans (1000 ppm) (RDA, 1989) and nonhuman primates (2200-6400 ppm) (NRC, 1978). One would presume that the howler's dietary requirement for sodium under the climatic conditions of the Venezuelan llanos would be slightly greater due to the high temperatures. In horses, prolonged exercise and elevated environmental temperatures increase the need for sodium because significant amounts are lost in sweat (NRC, 1989). The sodium concentration in natural feedstuffs for horses is often less than 0.1 percent (1000 ppm) (NRC, 1989). Although howlers may not sweat appreciably, they must either be very efficient in conserving limited dietary sodium or they acquire sodium from sources which were not included among the wild foods collected.

Consumption of soils (Izawa, 1993), or soils processed by termites (termitaria), by red howlers has been reported in

both French Guiana (Julliot and Sabatier, 1993) and Colombia (Izawa and Lozano, 1990). Although not observed in these studies, numerous reports exist in the literature concerning the consumption of soils (geophagia) by primates, including red leaf monkeys (Davies and Baillie, 1988), colobus (Mackey, 1978; Harrison and Hladik, 1986), and gibbons, gorilla, red colobus, and indris (Hladik and Guegen, 1974).

Two hypotheses are typically presented explaining this behavior. One hypothesis is the assumption that geophagia is associated with high intakes of tannins in folivorous primate diets, so that the chemical and physical properties of ingested soils may assist in adsorption and excretion of these secondary plant metabolites. Another hypothesis presumes that soils are consumed as a supplemental dietary source of minerals.

There is no NRC estimated requirement for selenium concentrations in the diet of primates. This trace element, which functions as an essential component of the enzyme glutathione peroxidase (Rotruck et al., 1973), is required by swine at 0.1 and 0.3 ppm (NRC, 1988) in the diet. The selenium requirement of the horse was estimated at 0.1 ppm of diet (Stowe, 1967). The concentration of selenium in most feedstuffs, which is a function of soil selenium content and pH, ranges from 0.05 to 0.3 ppm (NRC, 1989). Regions of Venezuela have been previously recognized as seleniferous

zones (Jaffe, 1976).

The average concentration of selenium (1.04 ppm) in the diet selected by red howlers was higher than anticipated. Although some foods were high in this element, this average concentration was well within the limits of safety for domestic animals (NRC, 1989).

CONCLUSION

The red howler found in the central llanos of Venezuela were strictly herbivorous. The dramatic seasonal changes in amounts of rainfall, and the impact of those changes on vegetation abundance and diversity is apparent. The diet of the red howler fluctuated with these seasonal changes, yet mature leaves were consistently the primary food item selected during all times of the year. The remainder of the diet, composed of fruit, flowers, and leaves in various stages of maturity, was consumed opportunistically as seasonally available.

Chemical analyses of the selected plant parts, including those parts previously stated to be "more readily digestible" indicate that the red howler of this region consumes a highly fibrous diet. The structure and capacity of the hindgut permit the retention of digesta required for extensive microbial fermentation of plant cell wall. That howlers consistently spend over 75% of their day resting suggests a

conservation of energy expenditure. This may be a result of the lower digestible energy content of the selected foods, devotion of metabolic energy to utilization of fermentation by-products, and/or detoxification of secondary plant metabolites.

The selected diet also provides moderate amounts of protein and minerals. Although the red howler would appear to be a perfect candidate to benefit from coprophagy, this behavior was not observed. The variability in mineral concentrations seen in range plants consumed by free-ranging ungulates was also observed in the plants selected by the red howlers.

The red howler, although not a strict folivore, is a highly folivorous and adaptable feeder. The adaptations of this species to a fibrous diet, as with most herbivores, are seen at all levels, behavioral, anatomical, and physiological. Each of these adaptations complements the others, permitting the species to maximize the food potential of the vegetation with which it has coevolved.

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COMPARATIVE ADAPTATIONS TO FOLIVORY
IN PRIMATES

Volume II

By

Mark Stephen Edwards

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Chapter III

Digestive Capabilities and Digesta Transit in Leaf-eating Primates

Feeding Habits of Folivorous Primates

It is difficult to generalize the feeding habits of primates whose diet consists, in part or entirely, of leaf material. Indeed, within the order Primates, a wide range of folivory is exhibited (Oftedal, 1991). Much of this variation is a reflection of the differences in gastrointestinal anatomy of these species (Oftedal, 1991; Chivers, 1994).

The interaction of plants and animals has been studied extensively. Green plants, which are autotrophic and can manufacture essential organic substances for life, supply the nutriment for herbivorous animals and other organisms that feed on those plants (Van Soest, 1982). Plants also have developed mechanisms of defense which protect the plant, or parts of the plant, from consumption by herbivores. One of these defenses is plant fiber.

Dietary fiber influences a number of factors including passage rates of food through the gastrointestinal tract and

digestibility of nutrients (Cummings, 1978). There are no established minimum requirements for plant fiber concentrations in the diet of domestic animals or humans (RDA, 1989). In fact, dietary fiber has often been considered a "negative feed factor" that diminishes the value of a feed for support of production. However, the presence of fiber in the diet of herbivores plays a very important role.

The reduction or removal of fiber from the diet can compromise an animal's health (Cummings, 1978). Alternatively, inclusion of dietary fiber at appropriate concentrations may reduce the occurrence of intestinal disorders (Morin et al., 1978; Ensley et al., 1982; Ullrey, 1986; Helstab, 1988; Janssen, 1994).

The relative contributions of plant materials and the plant parts selected by primates vary widely. Numerous field studies have examined the types of foods selected by free-ranging primates, and the manner in which these studies were conducted has been found to influence the results (See Chapter II).

Based on field observations, hanuman langurs (*Semnopithecus entellus*) were found to spend only 25.7% of the daytime feeding (Newton, 1992). Feeding time was divided among the following food items: mature leaves (34.9%), fruits (24.4%), leaf buds (10.6%), flowers and flower buds (9.5%), young leaves (3.6%), insects (3.0%), and plant exudates/gums

(1%). The ability of hanuman langurs to utilize plant materials, the consumption of which comprises 96% of the time spent feeding, is a reflection of the specialization of the animal's gastrointestinal tract.

Black and white colobus (*Colobus guereza*) have been studied extensively in their natural habitat. Guatier-Hion (1983) concluded, based upon analysis of the stomach contents of five animals, that their diet included $50.5 \pm 34\%$ leaf material, $49 \pm 34\%$ fruit and seeds combined, and 0.5% other materials. Leaves of all phenological stages were consumed. Based upon visual observations of feeding behavior, Clutton-Brock (1975) found that black and white colobus fed mostly on shoots, flowers, and fruit during a 3-mo period. Leaf selection appeared to be a function of seasonal availability, with highest levels of consumption occurring during the dry season.

Analyses were conducted of the nutrient composition of leaf parts from two tree species, *Celtis durandii* and *Markhamia platycalyx*, that were preferred as food by both red colobus and black and white colobus (Branga, 1982). It was found that there were marked differences in the nutrient content of young and mature leaves, with young leaves being preferred over mature leaves by both species. The young leaf blades of *Markhamia platycalyx* had higher crude protein (33.1% vs. 22.0%), lower ADF (47.9% vs. 55.6%), and lower ADL (15.8%

vs. 23.7%) concentrations than mature leaf blades. A similar pattern was seen in the young leaf blades of *Celtis durandii*, with higher crude protein (39.0% vs. 22.1%), lower ADF (27.5% vs. 37.5%) and lower ADL (9.7% vs. 11.5%) concentrations than in mature leaf blades. Branga (1982) concluded that the most likely factors affecting food preference of free-ranging colobus were nutrient composition, inhibitory compounds (i.e., tannins, lignins), and the seasonal availability of alternate food items.

The proboscis monkey (*Nasalis larvatus*) has been the subject of several studies focusing on natural diet (Kern, 1964; Kawabe and Mano, 1972; Salter et al., 1985; Yeager, 1989). Yeager (1989) indicated that proboscis monkeys utilize at least 55 different plant species as food, with a marked preference for *Eugenia* spp. Although diverse species were selected, 11 plants species contributed 75.1% of the diet based on time spent feeding (Yeager, 1989). Similar to findings with other folivorous primates, seasonal shifts in foods selected by proboscis monkeys, were largely a function of availability.

Very little information exists on the feeding habits of or the plant species selected by the douc langur (*Pygathrix nemaeus*) (Lippold, 1977). Recently, a list of plants that were observed to be selected by this primate has been published (Nhat et al., 1993). However, no indication was

given of the proportion that individual plants or plant species contributed to the total diet.

It is clear that the pregastric fermentation seen in leaf-eating primates of the subfamily Colobinae and the food choices of these species are similar to those of selective ruminants (Kuhn, 1964; Bauchop and Martucci, 1968; Bauchop, 1978; Chivers and Hladik, 1980; Chivers, 1994). The importance of plant fiber for the health and maintenance of normal gastrointestinal function in leaf-eating primates should not be overlooked.

Captive Feeding Studies

The numbers of controlled feeding studies that have actually examined the digestibility of feeds and/or the rates of digesta passage in leaf-eating primates are few. This may be due to the limited number of animals available for digestibility trials in captivity, the lack of physical facilities required for proper collection of excreta, and concerns that the dietary manipulation required for such studies might be unduly stressful. As a result, there are few studies in which herbivorous primates have been individually housed and fed a single food at maintenance.

The studies found in the literature were either restricted by small sample size or by an apparent lack of control over multiple variables. It should be noted that

these constraints are not unusual in nutrition studies conducted with captive wild animals. The limited number of specimens held in captivity and the complex social structure of primate groups makes removal of animals from established groups for short-term isolation during feeding trials very difficult. Also, the physical features of zoo exhibits often are not appropriate for the collection of digestibility data.

One of the first studies examining the digestive capabilities of leaf-eating primates involved the silvered langur (*Trachypithecus cristatus*) (Bauchop and Martucci, 1968). The focus of this study was measurement of the production of volatile fatty acids as a result of microbial fermentation of alfalfa. The authors reported that the animals maintained a pH (5.0- 6.7) in the foregut that would allow anaerobic bacteria to ferment ingested plant material. Although cellulolytic bacteria, such as a gram-positive coccus and a gram-negative *Bacteriodes* spp., were present in the forestomach of the langurs, no protozoa (characteristically present in ruminants) were found. Cellulolytic microorganisms produce end-products of fermentation that include ammonia, carbon dioxide, methane, and volatile short-chain fatty acids. These volatile fatty acids (VFAs), including acetic, butyric, and propionic acids, are primary source of energy for ruminant animals.

Fresh alfalfa was fed to the silvered langur (0 h), and

stomach contents were withdrawn via stomach tube at regular intervals (1, 1.5, 2, 2.5, 3.5, 4.5, 5.5, and 6.5 h). The VFA concentration peaked within 2 h after feeding, and held relatively constant over 6.5 h. Ammonia concentrations were also measured and were maintained at a high level, which the authors suggested was indicative of active bacterial proteolysis.

Another assessment of VFA concentrations in the gastrointestinal tract of captive leaf-eating monkeys involved the colobus monkey (*Colobus polykomos*) (Kay et al., 1976). Although balance trials were not conducted in this study, the progressive disappearance of food constituents along the entire length of the digestive tract was determined in two animals. The diet included only one item. This was a locally available exotic succulent, *Commelinum benghalense*. The two study subjects were sacrificed to determine the nutrient content of digesta at four points in the digestive tract.

Oxnard (1969) evaluated serum levels of vitamin B₁₂ in two species of langurs (*Trachypithecus obscurus*, *Semnopithecus entellus*). The concentrations (1000 to 3000 pg/ml) were high when compared with anthropoid primates (150 to 500 pg/ml) (Oxnard, 1966). He proposed that vitamin B₁₂ is synthesized by microbial organisms in the foregut of these langurs as seen in ruminant herbivores.

Milton et al. (1980) conducted two feeding trials with

wild-caught, mantled howler monkeys (*Alouatta palliata*) examining the digestibility of natural feedstuffs. Diet 1 consisted of 81% of four species of ripe fruits and 19% of *Cecropia insignis* leaves. Diet 2 consisted primarily (87%) of young leaves of different species and phenological stages and 13% of mixed species of fruits. The three animals used in the study, one adult male, one adult female, and one juvenile were housed individually; however, the variable nature of the diet was a primary limitation of the study.

Oftedal et al. (1982) examined dry matter intake and digestibility of a mixed-ingredient diet of constant composition that was fed to 2 black and white colobus monkeys (*Colobus guereza*). These animals were housed together, although both animals were similar in body weight (8.9 kg male, 8.8 kg female).

The acceptance of commercial primate biscuits, browse plants, and a produce mixture by a number of langur species including Francois' langurs (*Trachypithecus francoisi*), Douc langurs (*Pygathrix nemaeus*), hanuman langurs (*Semnopithecus entellus*), purple-faced langurs (*Trachypithecus vetulus*) and silvered langurs (*Trachypithecus cristatus*) was examined by Ullrey et al. (1982). The animals in this study were housed in groups of two to four individuals. The foods were offered in a manner that would permit differential selection by individual langurs, although the foods were weighed prior to

feeding. This study represents one of the most ambitious projects to date, yet the results were limited by the restrictions previously described.

Watkins et al. (1985) also examined the digestive capabilities of the black and white colobus (*Colobus guereza*). This study was one of the first to examine the acceptance and suitability of higher fiber primate biscuits, formulated to meet the specific needs of folivorous primates. Although this study also included a diet of mixed ingredients (Table 3-1), attempts were made to limit daily variability in intake by feeding fixed quantities of each food item at 95% of the animal's predetermined intake. Additionally, the two study subjects were individually housed, permitting collection of feces and orts without questions of their origin.

Table 3-1. Diet fed to two black and white colobus during pretrial and collection periods to determine digestibility (Watkins et al., 1985).

Feed group	Feed item
Commercial product	High fiber biscuit
Root vegetables	Sweet potato
Fruit	Apple
	Grapes
	Pear
	Orange
	Tomato
Green produce	Lettuce

Fiber digestion and digesta retention also were measured in silvered leaf monkeys (*Semnopithecus cristatus*) in a comparative study with Japanese (*Macaca fuscata*) and Rhesus macaques (*Macaca mulatta*) (Sakaguchi et al., 1991). Five adult langurs, each individually housed, were included in these trials. A single food item, a higher fiber "cubed" diet was offered *ad libitum* to the langurs in this study. The nutrient composition of the higher fiber "cubed" diet is provided in Table 3-2.

Measurements of food intake, digestion, and passage rate were made in captive proboscis monkeys at the New York Zoological Society (Dierenfeld et al., 1992). Although this is the only study in the literature in which attempts were made to quantify these measures in this species, this study has limitations that must be considered when interpreting the result.

Table 3-2. Concentrations of selected nutrients in a higher fiber "cubed" diet fed to silvered leaf monkeys (Sakaguchi et al., 1991).

Nutrient	Concentration (%)
Dry matter	91.9
Organic matter	81.4
Crude protein	18.3
Neutral detergent fiber	37.5
Acid detergent fiber	15.1

Unfortunately, all measurements were taken on a group of animals, one male and five females, that were not individually housed specimens. Therefore, variability between individuals or sexes cannot be isolated nor can individual intakes be quantified. Additionally, the animals were fed a mixed diet, the contents of which are outlined in Table 3-3. These compounding variables preclude the authors from drawing conclusions concerning food intake or digestibility.

A summary of digestibility trials conducted with leaf-eating primates is presented in Table 3-4. A summary of studies examining rates of digesta passage and retention is given in Table 3-5. Due to the diversity of foods used and the variable consumption of those foods, the variation in collection procedures and analytical techniques used, the variations in animal body weight and stages of growth, and the feeding of mixed diets, no attempt has been made to compare these individual experiments.

Digestive Markers

A variety of markers has been used to determine the rate of passage and/or retention of consumed food items by animals. Additionally, markers may be included in a diet to serve as an indirect indicator of digestibility. Markers can be classified by their function and characteristics (Table 3-6).

Table 3-3. Diet fed to a group of six (one male, five females) proboscis monkeys at the New York Zoological Park (Dierenfeld et al., 1992).

Food group	Food item
Browse plants	Alder
	Grape
	Mulberry
	Willow
	Mangrove
Green produce	Snap beans
	Broccoli
	Celery
	Kale
	Spinach
	Bok choy
Fruit	Sunflower sprouts
	Banana
	Plantain
Commercial products	Canned primate diet (Zu*Preem™)
	Dry biscuits (unspecified type)
Root vegetables	Carrots
	Yams
Miscellaneous	Eggs, hard-cooked
	Rice
	Peanut butter sandwich

Table 3-4. Apparent digestibility coefficients for dietary dry matter, fiber, and gross energy in various diets fed to leaf-eating primates and humans in previous studies.

Species	Diet type ^a	DM	NDF	ADF	ADL	GE	Author
Mantled howler	7	-	0.23	-	-	-	Milton et al., 1980
Mantled howler	8	-	0.41	-	-	-	Milton et al., 1980
Purple-faced langur	2	0.87	-	0.78	-	0.85	Ullrey et al., 1982
Purple-faced langur	4	0.84	-	0.72	-	0.81	Ullrey et al., 1982
Purple-faced langur	5	0.88	-	0.81	-	0.86	Ullrey et al., 1982
Purple-faced langur	6	0.88	-	0.74	-	0.87	Ullrey et al., 1982
Douc langur	2	0.81	-	0.80	-	0.78	Ullrey et al., 1982
Douc langur	4	0.81	-	0.71	-	0.78	Ullrey et al., 1982
Douc langur	5	0.83	-	0.78	-	0.82	Ullrey et al., 1982
Douc langur	6	0.85	-	0.73	-	0.82	Ullrey et al., 1982
Silvered langur	2	0.83	-	0.82	-	0.89	Ullrey et al., 1982
Silvered langur	4	0.85	-	0.70	-	0.81	Ullrey et al., 1982
Silvered langur	5	0.89	-	0.79	-	0.84	Ullrey et al., 1982
Silvered langur	6	0.90	-	0.73	-	0.87	Ullrey et al., 1982
Silvered langur	1	0.76	0.69	0.62	-	-	Sakaguchi et al., 1991

Table 3-4 (cont'd). Apparent digestibility coefficients for dietary dry matter, fiber, and gross energy in various diets fed to leaf-eating primates and humans in previous studies.

Species	Diet type ^a	DM	NDF	ADF	ADL	GE	Author
Black and white colobus	2	0.83	0.68	0.68	0.31	-	Oftedal et al., 1982
Black and white colobus	1	0.87	0.81	0.69	0.21	-	Watkins et al., 1985
Proboscis monkey (summer)	3	0.88	0.86	0.85	0.82	-	Dierenfeld et al., 1992
Proboscis monkey (winter)	3	0.89	0.86	0.86	0.82	-	Dierenfeld et al., 1992
Humans	LC	-	0.70	-	-	-	Slavin et al., 1981
Humans	HC	-	0.23	-	-	-	Slavin et al., 1981

^a1=nutritionally complete, higher fiber biscuit or cube.

2=mixed diet, including a standard primate biscuit, a canned primate diet, assorted green produce, root vegetables, and fruit.

3=mixed diet, including a standard primate biscuit and canned primate diet (11%), assorted browse and green produce (55%), root vegetables (9%), fruit (11%), and miscellaneous items (16%).

4=mixed diet, including a standard primate biscuit, *Eugenia* browse, assorted green produce, root vegetables, and fruit.

5=mixed diet, including a standard primate biscuit, *Hibiscus* browse, assorted green produce, root vegetables, and fruit.

6=mixed diet, including a standard primate biscuit, romaine lettuce, assorted green produce, root vegetables, and fruit.

7=ripe fruits (81%), including *Ficus yoponensis*, *F. insipida*, and young *Cecropia insignis* leaves (19%).

8=young leaves (87%), including *Ficus indipida*, *Cecropia insignis*, and immature fruits (13%), including *Cecropia insignis*, *C. obtusifolia*.

LC=low cellulose, including bread, fruits, vegetables, and refined grains.

HC=high cellulose, including bread with added Solka Floc (BW-200, Brown Co., Berlin, NH), fruits, vegetables, and refined grains.

Table 3-5. Transit time (TT_1), 50% recovery, and mean retention time (R_{GIT}) of various markers fed to leaf-eating primates.

Species	Diet type ^a	Marker type	TT_1 (h)	50% (h)	R_{GIT} (h)	Author
Spider monkey	3	plastic	4.4	-	-	Milton, 1981
Mantled howler	2, 3	plastic	20.4	-	-	Milton, 1981
Red howler	1	seed	21	54	134	Crissey et al., 1989
Proboscis monkey	4	bead	14	-	49	Dierenfeld et al., 1992
Silvered leaf monkey	1	Cr	13.6	-	46.8	Sakaguichi et al., 1991
Silvered leaf monkey	1	Co	13.6	-	44.8	Sakaguichi et al., 1991

^a1=nutritionally complete, higher fiber biscuit or cube.

2=ripe fruits (81%), including *Ficus yoponensis*, *F. insipida*, and young *Cecropia insignis* leaves (19%).

3=mixed diet, including bread, cottage cheese, green produce, and fruit.

4=mixed diet, including a standard primate biscuit and canned primate diet (11%), assorted browse and green produce (55%), root vegetables (9%), fruit (11%), and miscellaneous items (16%).

Table 3-6. Classification of markers used to evaluate rates of digesta passage (Kotb and Luckey, 1972).

Elements	
Inert metals (heavy & rare earth metals)	
Natural isotopes (^{40}K)	
Artificial isotopes (^{144}Ce)	
Compounds	
Inorganic	Metal oxides (Cr_2O_3)
	Mineral salts (BaSO_4)
Organic	Natural dyes (carmine, chromogen)
	Synthetic dyes (methylene blue)
	Other (lignin, cellulose, plant sterols)
Particulates	
Polymers	Polyethylene glycol, plastics, glass
Cells	Yeast, bacteria
Charcoal	
Metal particles	(e.g., sized aluminum particles)
Other particulates	Seeds, cotton string

The use of these markers in nutrition and physiological studies has been outlined by Kotb and Luckey (1972), and Udén (1978). Soluble markers must meet the following criteria, as modified by Udén (1978):

1. Be strictly nonabsorbable.
2. Not be subject to degradation or precipitation by the stomach or intestine.
3. Not be trapped by mucus or other gastrointestinal

contents during its flow through the intestine.

4. Not influence gastrointestinal motility.
5. Be easy to measure and give accurate results.
6. Have the same solubility characteristics as the test substance with which it might be used.
7. Not influence digestion.
8. Not interfere with the measurement of other substances.
9. Be measurable in opaque or strained samples.
10. Be estimated in very small concentrations thereby causing only a minimal osmotic disturbance.
11. Have the same "diffusion space" as the test substance.
12. Have the same physical characteristics as the fraction of interest during its residence in the gastrointestinal tract.
13. If used as a stain or mordant, should be firmly attached, and unaffected by digestion, pH, or other factors.
14. Be reasonable in price.

These specific requirements are more critical for markers used for rate of passage experiments than for markers used in balance trials (Udén et al., 1980).

MATERIALS AND METHODS

General

Four separate experiments were conducted at two zoological institutions, the Cleveland Metroparks Zoo (CMZ), Cleveland, OH, and the San Diego Zoo (SDZ), San Diego, CA. All trials were conducted between August 1992 and August 1993. The experimental protocol was coordinated within the established routines of daily animal care and exhibit or enclosure maintenance.

In vivo apparent digestibilities of dry matter, fiber fractions, and energy, rate of passage, and time of retention were measured for two diets of differing fiber concentrations. The experiments are listed in Table 3-7.

Table 3-7. Experimental feeding trials and data collected.

Experiment	Data collected
<i>In vivo</i> apparent digestibility	Total food intake, total fecal collection
Acetate bead marker	Rate of marker passage and retention
Co-EDTA marker	Rate of marker passage and retention
Cr-mordanted fiber marker	Rate of marker passage and retention

The staffs of both facilities were extremely cooperative

in providing individual housing of study subjects for the duration of the study. Each animal's response to the experimental procedure was monitored very closely. As a result, three individuals who failed to adapt to one of the two test diets were removed from that portion of the trial. A fourth animal was never integrated into the study because of inadequate consumption of the test diet. The welfare of these animals, all of which were endangered species, was considered paramount.

In each experiment, a cross-over design was used so that each individual might consume each of the test diets. Although the intention was to allow all individuals to remain in the study until completion, some individuals were removed from the study prior to the final collection, for reasons unrelated to the experimental treatments.

Test Diet Formulation

Two test diets formulated to offer a medium and high level of fiber were designated 15ADF and 30ADF, respectively, in reference to their targeted acid-detergent fiber (ADF) concentrations. Both diets were formulated to be nutritionally complete, meeting the estimated nutrient requirements of both New and Old World Primates for maintenance (NRC, 1978). The diets were manufactured as

extruded morsels approximately 27 x 15 x 5 mm (Marion Zoological, Inc., Plymouth, MN 55441). No additional food items were offered.

The two diets were made of the same ingredients, using variations in proportions of soy hulls and corn grain to produce the desired fiber concentrations. The composition of the two test diets is given in Table 3-8. The fiber concentration of the two test diets was the principal variable. The estimated concentrations of selected nutrients in the diets are presented in Table 3-9.

A sample of each test diet was ground in a Wiley mill fitted with a 2-mm screen. The samples were analyzed for dry matter (DM), ash, gross energy (GE), neutral-detergent fiber (NDF), ADF, cellulose (C), hemicellulose (HC), acid-detergent lignin (ADL), Ca, P, Mg, Na, K, Fe, Mn, Zn, and Se.

Animals, Housing, Feeding, and Collection of Excreta During Digestion Trials and Handling of Samples

Ten separate species/subspecies were used. Their scientific and common names are listed in Table 3-10. Based on records of previous physical examinations and current medical status, there were no apparent health problems with these animals.

Table 3-8. Composition (percentage by weight, air-dry basis) of the lower and higher fiber test diets.

Ingredient	Diet	
	15ADF	30ADF
Soybean meal (48% crude protein)	13.00	5.00
Corn gluten meal	11.00	15.00
Corn grain	24.00	---
Sugarbeet pulp	5.00	5.00
Soybean hulls	19.762	52.762
Corn hominy feed	10.00	5.00
Sucrose	10.00	10.00
Soybean oil	3.00	3.00
Dicalcium phosphate	1.85	2.20
Calcium carbonate	0.80	0.45
L-Lysine (78%)	0.30	0.30
Sodium chloride	0.50	0.50
Vitamin-trace mineral premix ^a	0.50	0.50
Mold inhibitor ^b	0.10	0.10
Red cabbage extract (color)	0.10	0.10
Vitamin C (ethocel coated)	0.05	0.05
Feed flavor	0.038	0.038

^aFormulated to provide per kg of diet: 8000 IU vitamin A, 1750 IU vitamin D₃, 250 IU vitamin E, 5 mg menadione, 3 mg thiamin, 4 mg riboflavin, 22.5 mg niacin, 1 mg pyridoxine, 0.1 mg biotin, 15 mg D-Ca-pantothenate, 0.3 mg folic acid, 25 mcg vitamin B₁₂, 200 mg choline, 25 mg Fe, 10 mg Cu, 90 mg Zn, 45 mg Mn, 1 mg I, 0.23 mg Se.

^b MonoProp™ (50% propionic acid on verxite), Anitox Corp., Buford, GA.

Table 3-9. Estimated nutrient concentrations (dry matter basis) of the test diets.

Nutrient	Diet	
	15ADF	30ADF
Dry matter (%)	91.2	91.7
Gross energy (kcal/g)	4.46	4.39
Crude protein (%)	20.5	20.0
Lysine (%)	1.1	1.0
Ether extract (%)	5.9	5.2
Ash (%)	6.1	6.7
Neutral-detergent fiber (%)	24.0	42.0
Acid-detergent fiber (%)	15.0	29.6
Acid-detergent lignin (%)	1.2	1.5
Crude fiber (%)	10.8	22.5
Calcium (%)	1.0	1.1
Phosphorus (%)	0.7	0.7

All animals were housed individually for the duration of the study. Every attempt was made to house conspecifics in adjacent enclosures to permit continued visual, olfactory, and vocal communication. However, due to the nature of the study, isolation for measurement of individual feed consumption and fecal output was necessary.

CMZ animals were housed indoors. SDZ animals were housed outdoors, with the exception of *Pygathrix nemaeus nemaeus*, *Colobus guereza kikuyuensis*, *Cercocebus galeritus chrysogaster*, and *Mandrillus leucophaeus leucophaeus* which had

free access to indoor/outdoor enclosures, except during cleaning and collection procedures. The enclosures varied in size and offered a variety of climbing structures. Concrete flooring was present in all enclosures.

Table 3-10. Scientific and common names of species included in the study.

Family/ subfamily	Scientific name	Common name
Lemuridae	<i>Varecia variegata rubra</i>	Red ruffed lemur
	<i>Varecia variegata variegata</i>	Black & white ruffed lemur
Alouattinae	<i>Alouatta caraya</i>	Black howler
	<i>Alouatta palliata</i>	Mantled howler
	<i>Alouatta seniculus sara</i>	Red howler
Colobinae	<i>Colobus guereza kikuyensis</i>	Black & white colobus
	<i>Trachypithecus francoisi francoisi</i>	Francois' langur
	<i>Pygathrix nemaeus nemaeus</i>	Douc langur
Cercopithecinae	<i>Cercocebus galeritus chrysogaster</i>	Golden-bellied mangabey
	<i>Mandrillus leucophaeus leucophaeus</i>	Drill

The animals had free access to water. Feed intake was monitored daily. Over a 4-wk period, animals were gradually converted from the mixed diets (which included commercially

available foods, produce, and browse) fed prior to the study to the test diets. The test diets were incrementally added to the daily diet, as the previously fed items were removed.

During preliminary trials and the conversion period, the quantities of test diets offered were increased until each animal was leaving 30 to 50 g daily to ensure *ad libitum* intake. Weighed quantities of the test diet were offered daily at approximately 0900 h. After approximately 24 h, remaining quantities of food (orts) were collected and weighed. The test diets were fed exclusively for a minimum of 1 wk (adaptation period) prior to the 1st d of fecal collection.

Following the adaptation period, feces were collected for 14 d. All feces were collected daily during the morning cleaning procedures using a plastic putty knife. Daily fecal samples were kept separate. Collected feces were sealed in plastic bags to prevent moisture loss and stored at 0°C prior to analysis. Urine was not collected and no attempt was made to prevent urinary contamination of the fecal material. Due to the arboreal habits of these primates, urinary contamination was not a primary concern.

Chemical Analysis of Feed and Feces

The weight of the frozen fecal material was recorded and

all samples were freeze-dried in preparation for analysis. Following freeze-drying, samples were reweighed, crushed into a fine powder, and thoroughly mixed. Test diets and feces were analyzed for DM, GE, NDF, ADF, and ADL. Total moisture/dry matter concentration was determined using the freeze-dried DM and a final DM. The final DM was determined on approximately a 1.0-g freeze-dried subsample in an aluminum weighing dish by overnight drying in a vacuum oven at 60°C. Gross energy was determined by complete combustion of an approximately 1-g sample in a Parr adiabatic oxygen bomb calorimeter (Parr Instrument Co., Moline, IL). Following combustion, the remaining residue was titrated with 0.0725 N sodium carbonate to correct for the heat of formation of nitric and sulfuric acids. Sequential fiber analysis as described by Goering and Van Soest (1970) was used to determine NDF, ADF, and ADL. Sequential analysis produces lower AD-nitrogen values (Udén, 1978). Sulfite was not used in the ND treatment because it solubilized part of the lignin. When sulfite was not used, somewhat higher NDF-nitrogen values resulted. Approximately a 0.5-g subsample was used for the procedure. A 2% α -amylase (A-3051, Sigma Chemical Co., St. Louis, MO) solution was used in the NDF analysis (Robertson and Van Soest, 1977). The NDF residue was treated with acid detergent (AD) to determine ADF. ADL was determined on the

ADF residue using 72% sulfuric acid (Goering and Van Soest, 1970). ADL residue was ignited at 500°C in a muffle furnace to determine the AD-insoluble ash residue. The fiber residues were calculated as follows (Udén, 1978):

ND residue - AD residue = hemicellulose

AD residue - AD lignin = cellulose

AD lignin - AD-insoluble ash residue = lignin

All analyses were performed in duplicate.

Apparent dry matter digestibility (ADMD) and digestibility of dietary components, fiber, and energy were estimated according to the simple relationship:

$$\text{ADMD} = \frac{(\text{Total consumed} - \text{Total excreted in feces})}{\text{Total consumed}} \times 100$$

When possible, the animals were weighed at the beginning of the study, during the crossover transition period, and at the end of the study. Individual animals were moved into plastic airline kennels and weighed on an electronic balance. Recently recorded weights obtained from medical records were used for those individuals who would be unacceptably stressed by the weighing procedure.

RATE OF DIGESTA PASSAGE MEASUREMENTS

Rate of passage experiments using acetate beads were conducted in conjunction with digestibility trials. Co-EDTA and Cr-mordanted fiber trials were conducted separately.

Marker Administration and Sampling Frequency

Inducing domestic animals to consume markers at the desired time can lead to a variety of problems. Encouraging primates to consume these markers produced an entirely new set of obstacles. All markers were mixed with ground test diet (≤ 20 g) and fruit nectar (typically mango, ≤ 25 g) to enhance palatability. The fruit nectar also provided adequate moisture to hold the marker/test diet mixture together. The dough-like mixture was rolled into balls, placed into individually labeled bags, and hand-fed to each subject.

Co-EDTA (14.35% Co) was dosed orally at 0.50 g per individual, providing 71.75 mg Co. Cr-mordanted fiber was fed in quantities to deliver 40 mg Cr to the test subject.

These methods were successful, but a few individuals continued to refuse the marker after several attempts. Thus, the marker was placed in a small portion (≤ 10 g) of either white grape or banana. The marker was consumed by

most of the remaining animals using these vehicles.

Every attempt was made to feed the markers to each individual within the hour from 0900 to 1000 h. Only when an individual refused the initial attempt was a follow-up attempt made the following day, during the same time period (0900-1000 h).

All feces were collected. Following the introduction of the markers, feces were collected at 3-h intervals. The collections from the study subjects were made in the same order that the markers were fed. A post-dusk sample was collected at 2100 h and a pre-dawn sample was collected at 0300 h. Fecal samples were not collected or observed at 0000 h, so as not to disrupt the animals during the night. This collection schedule was continued for 2 wk following introduction of the marker.

Samples were immediately transferred to plastic storage bags upon collection and stored at 0°C until analyzed.

Marker Synthesis and Mordanting of Plant Fiber

Co-EDTA

Udén (1978) found that a Li Co-EDTA salt produce diarrhea in some sheep and goats, but the Na Co-EDTA did not yield similiar conditions. For that reason, a Na Co-EDTA salt was selected as a liquid marker for all liquid phase digesta

transit experiments.

The Na Co-EDTA was synthesized using an adaptation of the procedure described by Udén (1978) as follows:

1. Weigh 25 g of Co(II)acetate•4H₂O (cobaltous acetate), 29.2 g EDTA (ethylenediaminetetraacetic acid), 4.0 g sodium hydroxide, and 200 ml of distilled water into a 2-L beaker.
2. Record initial volume. Dissolve, stirring continuously with moderate heat (if necessary) for 4 to 5 h.
3. Discontinue heat and restore to the initial volume with ddH₂O (double distilled water). Stir overnight.
3. Place beaker in ice bath on stir plate to permit continued stirring. Add **SLOWLY** 20 ml of hydrogen peroxide (30% solution). **** CAUTION: WILL FOAM OVER IF TOO MUCH HYDROGEN PEROXIDE IS ADDED AT ONCE. ****
4. Remove from ice bath. Continue stirring for 5 to 6 h.
5. Divide equally into two 2-L beakers.
6. Add 150 ml ethanol (95% v/v) to each beaker. Leave at room temperature for 1 to 2 h. Refrigerate overnight (or longer). NOTE: Longer period of refrigeration, such as a weekend, will increase final

yield.

7. Filter on a large Buechner funnel under vacuum and wash with ethanol (80% v/v).
8. Equilibrate with moisture in air for 24 h.
9. Place in a storage container. Take a sample (5 g) for Co assay.

Cr-mordanted fiber

Chromium was used as the particulate marker in all solid-phase digesta transit trials. Chromium has been described as one of the easiest particulate markers with which to work, inexpensive, easy to analyze, easy to mordant, and accepted as a safe marker for human studies (Udén, 1978). Cr-mordanted fiber has been shown to be indigestible (Martz et al., 1974).

The Cr was mordanted to a macroamount of NDF from each of the test diets. The procedure for mordanting Cr to the plant fiber was as follows (modification of Uden et al., 1980):

1. Prepare a macroamount of plant cell wall by boiling in neutral detergent (ND) solution for 1 h, approximately 50 g of diet per 1 L of ND solution.
2. Rinse thoroughly with hot ddH₂O through a brass sieve followed by a rinse with acetone.
3. Place in a 65°C oven until dry.

4. Weigh cell wall fraction.
5. Add a water solution providing 375 g sodium dichromate ($\text{Na}_2\text{Cr}_2\text{O}_7$) for every 1000 g of plant fiber (an amount of chromium equivalent to 10% of the amount of fiber used) in amounts sufficient to cover the fiber.
6. Boil cell wall fraction at 100°C for 3 h.
7. Wash the fiber thoroughly with tap water.
8. Suspend the fiber in tap water and add ascorbic acid equivalent to 50% of the weight of plant cell wall (the liquid should taste slightly sour). Let soak for at least 1 h.
9. If the fiber has turned green, rinse until free of soluble material and dry at 65°C in a forced-draft oven.

Analysis of Markers

Frozen samples were weighed, freeze-dried, and reweighed. The freeze-dried samples were crushed to a fine powder and thoroughly mixed. Ten samples were randomly selected from the 14-d collection period to determine DM using approximately a 1.0-g subsample in an aluminum weighing dish by overnight drying in a vacuum oven at 60°C . Freeze-dried feces were digested with nitric-perchloric acid (Fenton and

Fenton, 1979). Concentrated nitric acid (20.0 ml) and 70% perchloric acid (5.0 ml) were added to 1 g of ground sample in a Phillip's beaker. The sample was digested until 1 ml of acid was left in the beaker. Following digestion, the samples were diluted with ddH₂O. All samples were digested in duplicate, unless a small sample size demanded otherwise.

All samples were analyzed using an atomic absorption/emission spectrophotometer (Smith-Hieftje 4000, Thermo-Jarrell Ash). Chromium samples were analyzed in a high-temperature nitrous oxide/acetylene flame with the emission wavelength set at 425.4 nm. Cobalt samples were analyzed in an air/acetylene flame with the absorption wavelength at 240.7 nm. All analyses were performed in duplicate.

Mathematical Calculations of Retention Time, Transit Time, and Rate Constants.

The mean retention time, including transit time ($R_{GIT} + TT$), was calculated according to Blaxter et al. (1956).

$$R_{GIT} + TT = \frac{\sum (Y_i \cdot t_i)}{\sum Y_i}$$

Transit time (TT) was determined as the time between dosing and first appearance of the marker in the feces. R_{GIT} was determined by subtracting TT from $R_{GIT} + TT$.

Statistical analyses were completed using QuattroPro (Novell Applications Group, Orem, UT). Comparisons among

gastrointestinal tract type within diet were made using a one-way analysis of variance. Comparisons between diets within the gastrointestinal tract group were made by paired t-test.

RESULTS

Body weights of all individuals before, during, and following the trials are shown in Appendix Table B1. The results from the digestibility trials for each individual are shown in Appendix Tables B2-B12. The results from the digesta marker trials for each individual are shown in Appendix Tables B13-B19. The digestibility and marker results for the single golden-bellied mangabey and drill are not included in the statistical analyses but can be found in Appendix Tables B17, B18, and B19, respectively.

Body Weight Changes

The body weights of *Varecia variegata* were significantly lower when maintained on diet 30ADF than when consuming diet 15ADF ($P < 0.01$). There were no statistically significant differences ($P > 0.05$) among the body weights of the two other groups, *Alouatta* spp. and colobine primates, fed diets 15ADF or 30ADF (Table 3-11).

The mean body weights of species and/or subspecies included in statistical analyses are shown in Table 3-12.

Table 3-11. Mean body weight (BW) and mean dry matter intake (DMI) of primate study subjects fed diets 15ADF and 30ADF grouped by gastrointestinal tract (GIT) type.

GIT Type/Species	Diet	n	BW (kg)	DMI (g/d)	DMI (g/kg BW)	DMI (% BW)
SIMPLE GIT						
<i>Varecia variegata</i> spp.	15ADF	5	4.68 ^a	136.3 ^c	29.0 ^a	2.90 ^a
	30ADF	5	4.04 ^b	222.6 ^d	54.9 ^b	5.49 ^b
HINDGUT FERMENTER						
<i>Alouatta</i> spp.	15ADF	7	7.52	132.4	18.9	1.89
	30ADF	7	7.61	161.9	22.4	2.24
FOREGUT FERMENTER						
<i>Colobus</i> , <i>Pygathrix</i> , <i>Trachypithecus</i>	15ADF	7	7.54	213.7	29.7	2.97
	30ADF	7	7.46	204.0	28.6	2.86

^{a,b} Values in same column with different superscripts differ ($P < 0.01$).

^{c,d} Values in same column with different superscripts differ ($P < 0.05$).

Table 3-12. Mean body weight (BW) and mean dry matter intake (DMI) of primate study subjects fed diets 15ADF and 30ADF grouped by species/subspecies.

Species	Diet	n	BW (kg)	DMI (g/d)	DMI (g/kg BW)	DMI (% BW)
<i>Varecia variegata rubra</i>	15ADF	3	4.58	139.0	30.0	3.00
	30ADF	3	4.00	183.8	45.6	4.56
<i>Varecia variegata variegata</i>	15ADF	2	4.83	132.4	27.5	2.75
	30ADF	2	4.10	280.8	68.8	6.88
<i>Alouatta caraya</i>	15ADF	3	8.11	128.0	17.6	1.76
	30ADF	3	8.11	185.1	25.5	2.55
<i>Alouatta villosa palliata</i>	15ADF	2	5.85	141.0	23.9	2.39
	30ADF	2	6.45	131.5	20.3	2.03
<i>Alouatta seniculus sara</i>	15ADF	2	8.32	130.6	16.1	1.61
	30ADF	2	8.03	157.7	19.7	1.97
<i>Colobus guereza kikuyuensis</i>	15ADF	1	10.90	154.8	14.2	1.42
	30ADF	1	10.70	153.8	14.4	1.44
<i>Pygathrix nemaeus nemaeus</i>	15ADF	1	12.10	428.9	35.5	3.55
	30ADF	1	11.75	391.1	33.3	3.33
<i>Trachypithecus f. francoisi</i>	15ADF	5	5.96	182.4	31.6	3.16
	30ADF	5	5.94	176.6	31.8	3.18

Dry Matter Intake

Dry matter intakes were expressed as grams of dry matter consumed per d (24 h), and as a function of the animal's body weight, g/kg BW or %BW. Statistically significant differences between diets 15ADF and 30ADF were observed only in *Varecia variegata* spp. Dry matter intakes of diet 30ADF by *Varecia variegata* spp. were statistically higher than of diet 15ADF when expressed as g/d ($P < 0.05$) and as a function of body weight ($P < 0.01$). However, there were no statistical differences ($P > 0.05$) between the dry matter intakes of either diet by *Alouatta* spp. or the colobine species (Table 3-11).

The mean dry matter intakes of species and/or subspecies included in the statistical analyses are shown in Table 3-12.

Apparent Dry Matter Digestibility

The apparent dry matter digestibility (ADMD) of diet 30ADF by both *Varecia variegata* and colobine species was statistically ($P < 0.05$) lower than that of diet 15ADF. The ADMD of diet 30ADF by *Alouatta* spp. was also significantly ($P < 0.01$) lower than that of diet 15ADF (Table 3-13). Statistically significant differences were observed in ADMD between gastrointestinal tract type (simple, hindgut, foregut), within either diet 15ADF or 30ADF ($P < 0.0005$).

The mean ADMD of diets 15ADF and 30ADF by species and/or

Table 3-13. Mean apparent dry matter digestibility (DMD), digestible energy (DE) of diets 15ADF and 30ADF, and digestible energy intake (DEI) for primate study subjects grouped by gastrointestinal tract (GIT) type.

GIT Type/Species	Diet	n	DMD (%)	DE (%)	DE (kcal/g)	DEI (kcal/kg ^{0.75})
SIMPLE GIT						
<i>Varecia variegata</i> ssp.	15ADF	5	51.0 ^{a,e}	47.0	2.20	92.80
	30ADF	5	41.7 ^{b,e}	39.7	1.74	134.49
HINDGUT FERMENTER						
<i>Alouatta</i> spp.	15ADF	7	69.3 ^{c,f}	68.5 ^c	3.05	92.74
	30ADF	7	61.7 ^{d,f}	61.5 ^d	2.70	98.16
FOREGUT FERMENTER						
<i>Colobus, Pygathrix, Trachypithecus</i>	15ADF	7	81.2 ^{c,g}	80.9 ^c	3.61	173.79
	30ADF	7	76.6 ^{d,g}	75.6 ^d	3.32	152.31

^{a,b} Values in same column with different superscripts differ ($P < 0.05$).

^{c,d} Values in same column with different superscripts differ ($P < 0.01$).

^{e,f,g} Values in same column with different superscripts differ ($P < 0.0001$).

subspecies shown in the statistical analyses are included in Table 3-14.

Energy Digestibility and Energy Intake

The digestible energy (DE) of diet 30ADF was significantly ($P < 0.01$) lower than that of diet 15ADF for both the colobine species and *Alouatta* spp. No statistically significant differences were demonstrated between diets 15ADF and 30ADF fed to *Varecia variegata* (Table 3-13).

The mean DE (% or kcal/g) of diets 15ADF and 30ADF, and DE intake (kcal/kg^{0.75}) by species and/or subspecies included in the statistical analyses are shown in Table 3-14.

Fiber Component Digestibility

No statistical differences were seen in the digestibility of the individual cell wall components (NDF, ADF, C, HC, ADL) between diets 15ADF and 30ADF within each gut type ($P < 0.01$), except for the digestibility of HC by *Alouatta* spp., which was significantly ($P < 0.01$) lower in diet 15ADF than in diet 30ADF (Table 3-15).

The mean percent digestibility of various fiber components (NDF, ADF, C, HC) in diets 15ADF and 30ADF by species and/or subspecies included in the statistical analyses are shown in Table 3-16.

Table 3-14. Mean apparent dry matter digestibility (DMD), digestible energy (DE) of diets 15ADF and 30ADF, and digestible energy intake (DEI) for primate study subjects grouped by species/subspecies.

Species	Diet	n	DMD (%)	DE (%)	DE (kcal/g)	DEI (kcal/kg ^{.75})
<i>Varecia variegata rubra</i>	15ADF	3	53.3	48.8	2.18	94.35
	30ADF	3	41.2	39.1	1.71	108.44
<i>Varecia variegata variegata</i>	15ADF	2	47.7	44.4	2.25	90.45
	30ADF	2	42.5	40.8	1.79	173.57
<i>Alouatta caraya</i>	15ADF	3	67.7	66.4	2.96	83.72
	30ADF	3	62.0	61.6	2.70	111.33
<i>Alouatta villosa palliata</i>	15ADF	2	70.0	68.8	3.07	114.12
	30ADF	2	62.1	61.8	2.71	87.80
<i>Alouatta seniculus sara</i>	15ADF	2	71.0	71.5	3.19	84.89
	30ADF	2	61.8	61.1	2.68	88.78
<i>Colobus guereza kikuyuensis</i>	15ADF	1	80.3	78.5	3.50	90.28
	30ADF	1	78.7	78.0	3.42	89.01
<i>Pygathrix nemaeus nemaeus</i>	15ADF	1	76.2	81.6	3.64	240.92
	30ADF	1	73.9	72.5	3.18	195.95
<i>Trachypithecus f. francoisi</i>	15ADF	5	82.4	81.2	3.62	177.07
	30ADF	5	76.7	75.7	3.32	156.25

Table 3-15. Mean digestibility (%) of various fiber components (NDF, ADF, C, HC) in diets 15ADF and 30ADF for primate study subjects grouped by gastrointestinal tract (GIT) type.

GIT Type/Species	Diet	n	NDF	ADF	C	HC
SIMPLE GIT						
<i>Varecia variegata</i> spp.	15ADF	5	20.4	9.4	11.5	38.8
	30ADF	5	20.7	12.6	8.7	38.9
HINDGUT FERMENTER						
<i>Alouatta</i> spp.	15ADF	7	44.8	42.2	39.2	50.3 ^a
	30ADF	7	47.4	40.6	39.1	62.4 ^b
FOREGUT FERMENTER						
<i>Colobus, Pygathrix, Trachypithecus</i>	15ADF	7	77.1	79.7	80.4	71.9
	30ADF	7	74.7	71.3	75.2	77.0

^{a,b} Values in same column with different superscripts differ ($P < 0.01$).

Table 3-16. Mean digestibility (%) of various fiber components (NDF, ADF, C, HC) in diets 15ADF and 30ADF for primate study subjects grouped by species/subspecies.

Species	Diet	n	NDF	ADF	C	HC
<i>Varecia variegata rubra</i>	15ADF	3	22.9	12.1	15.9	40.3
	30ADF	3	19.0	10.6	6.6	38.0
<i>Varecia variegata variegata</i>	15ADF	2	16.6	5.3	5.9	36.5
	30ADF	2	23.3	15.8	11.9	40.3
<i>Alouatta caraya</i>	15ADF	3	46.5	40.5	38.0	53.6
	30ADF	3	45.8	37.7	36.8	63.6
<i>Alouatta villosa palliata</i>	15ADF	2	43.7	43.8	39.5	51.8
	30ADF	2	52.5	46.2	44.5	66.8
<i>Alouatta seniculus sara</i>	15ADF	2	43.4	43.1	40.8	43.8
	30ADF	2	44.8	39.5	37.3	56.4
<i>Colobus guereza kikuyuensis</i>	15ADF	1	77.0	80.1	81.4	67.9
	30ADF	1	74.3	56.2	76.1	78.0
<i>Pygathrix nemaeus nemaeus</i>	15ADF	1	66.5	66.6	59.7	66.4
	30ADF	1	69.8	67.6	66.1	74.8
<i>Trachypithecus f. francoisi</i>	15ADF	5	79.3	82.3	84.3	73.7
	30ADF	5	75.7	75.0	76.9	77.3

Markers

There was no statistical difference ($P > 0.01$) seen in either TT_1 (Table 3-17) or R_{GIT} (Table 3-19) between diets 15ADF and 30ADF for acetate bead markers, Co-EDTA, and Cr-mordanted fiber fed to *Varecia variegata*, *Alouatta* spp. or the colobine species. Unfortunately, due to previously mentioned circumstances, eight animals had to be removed from the second Cr-fiber trial, thus eliminating them from the statistical analyses. The results of the first Cr-fiber trial for these animals are provided in the Appendix (B15-B16).

The mean TT_1 and R_{GIT} of species and/or subspecies fed diets 15ADF and 30ADF and included in the statistical analyses are presented in Tables 3-18 and 3-20, respectively.

Markers (acetate bead, Co-EDTA, and Cr-mordanted fiber) were compared to each other in order to determine the level of correlation for parameters measured (TT_1, R_{git}). TT_1 and R_{git} as estimated by different markers within diet 15ADF or 30ADF were not significantly correlated.

Discussion

General

Fermentation of the plant cell wall is a relatively slow process, requiring the retention of digesta in specific segments of the gastrointestinal tract (Parra, 1978). The rate at which digesta transit the tract is influenced by

Table 3-17. Mean transit time (TT_i, h) of various markers, acetate bead, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primate study subjects grouped by gastrointestinal tract (GIT) type.

GIT Type/Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
SIMPLE GIT				
<i>Varecia variegata</i> spp.	15ADF	3.0 (6) ^a	2.7 (5)	2.1 (5)
	30ADF	2.5 (6)	2.7 (5)	2.7 (5)
HINDGUT FERMENTER				
<i>Alouatta</i> spp.	15ADF	32.3 (4)	15.6 (7)	23.3 (4)
	30ADF	24.8 (4)	16.1 (7)	15.8 (4)
FOREGUT FERMENTER				
<i>Colobus, Pygathrix, Trachypithecus</i>	15ADF	31.5 (2)	16.5 (6)	46.5 (1)
	30ADF	37.5 (2)	21.0 (6)	43.5 (1)

^an in parentheses

Table 3-18. Mean transit time (TT₁, h) of various markers, acetate beads, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primate study subjects grouped by species/subspecies.

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
<i>Varecia variegata rubra</i>	15ADF	2.5 (3) ^a	3.5 (3)	2.5 (3)
	30ADF	3.5 (3)	2.5 (3)	3.5 (3)
<i>Varecia variegata variegata</i>	15ADF	3.0 (2)	1.5 (2)	1.5 (2)
	30ADF	1.5 (2)	3.0 (2)	1.5 (2)
<i>Alouatta caraya</i>	15ADF	-	16.5 (3)	-
	30ADF	-	9.5 (3)	-
<i>Alouatta villosa palliata</i>	15ADF	18.0 (2)	7.5 (2)	12.0 (2)
	30ADF	13.1 (2)	7.5 (2)	4.5 (2)
<i>Alouatta seniculus sara</i>	15ADF	46.5 (2)	22.5 (2)	34.5 (2)
	30ADF	36.0 (2)	34.5 (2)	27.0 (2)
<i>Colobus guereza kikuyuensis</i>	15ADF	31.5 (1)	43.5 (1)	46.5 (1)
	30ADF	31.5 (1)	43.5 (1)	43.5 (1)
<i>Pygathrix nemaeus nemaeus</i>	15ADF	31.5 (1)	1.5 (1)	1.5 (1)
	30ADF	43.5 (1)	19.5 (1)	-
<i>Trachypithecus f. francoisi</i>	15ADF	-	13.5 (4)	-
	30ADF	-	15.8 (4)	-

^an in parentheses.

Table 3-19. Mean retention time (R_{git} , h) of various markers, acetate bead, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primate study subjects grouped by gastrointestinal tract (GIT) type.

GIT Type/Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
SIMPLE GIT				
<i>Varecia variegata</i> spp.	15ADF	5.2 (6) ^a	4.1 (5)	3.8 (5)
	30ADF	4.9 (6)	2.4 (5)	2.3 (5)
HINDGUT FERMENTER				
<i>Alouatta</i> spp.	15ADF	30.1 (4)	34.1 (7)	38.8 (4)
	30ADF	24.2 (4)	40.4 (7)	38.8 (4)
FOREGUT FERMENTER				
<i>Colobus</i> , <i>Pygathrix</i> , <i>Trachypithecus</i>	15ADF	30.7 (1)	41.1 (6)	37.6 (1)
	30ADF	37.6 (1)	38.4 (6)	68.6 (1)

^an in parentheses.

Table 3-20. Mean retention time (R_{ret} , h) of various markers, acetate beads, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primate study subjects grouped by species/subspecies.

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
<i>Varecia variegata rubra</i>	15ADF	3.8 (3) ^a	4.0 (3)	3.1 (3)
	30ADF	6.3 (3)	3.3 (3)	5.0 (3)
<i>Varecia variegata variegata</i>	15ADF	2.2 (2)	4.3 (2)	1.6 (2)
	30ADF	2.3 (2)	1.1 (2)	3.4 (2)
<i>Alouatta caraya</i>	15ADF	-	18.4 (3)	-
	30ADF	-	38.4 (3)	-
<i>Alouatta villosa palliata</i>	15ADF	25.7 (2)	33.6 (2)	37.8 (2)
	30ADF	25.4 (2)	30.6 (2)	36.8 (2)
<i>Alouatta seniculus sara</i>	15ADF	34.5 (2)	58.2 (2)	39.9 (2)
	30ADF	22.9 (2)	53.3 (2)	40.8 (2)
<i>Colobus guereza kikuyuensis</i>	15ADF	20.7 (1)	44.0 (1)	37.6 (1)
	30ADF	37.6 (1)	53.4 (1)	68.6 (1)
<i>Pygathrix nemaeus nemaeus</i>	15ADF	-	35.5 (1)	33.8 (1)
	30ADF	-	32.5 (1)	-
<i>Trachypithecus f. francoisi</i>	15ADF	-	41.1 (4)	-
	30ADF	-	36.1 (4)	-

^a n in parentheses.

factors such as diet composition, rate of digestion, and level of intake (Allen and Mertens, 1988; Church, 1988). The effect of intake on dietary digestibility is much more pronounced when an animal is fed a mixed-ingredient diet than one composed of a single food, as in this study. In general, as intake increases, dry matter digestibility is depressed as a consequence of an increased rate of digesta passage through the gastrointestinal tract. The depression of digestibility related to increased intake is not limited to fiber but also includes more readily fermentable components of the diet such as starch.

Digesta transit time in herbivores, when compared across dietary and gastrointestinal types, tends to decrease from ruminants to nonruminants with hindgut fermentation to more generalist feeders (e.g., omnivores). The rate of passage in herbivores generally increases with decreasing body size (Parra, 1978). It is generally believed that nonruminant herbivores exhibit a faster rate of passage and a shorter mean retention time as compared to foregut fermenters (ruminants) (Moir, 1968; Parra, 1978).

It is apparent that these factors are closely inter-related and dependent upon one another. The level of intake influences transit time, and thus influences digestibility. In turn, the digestibility of the diet influences the level of intake. These are the complex relationships that make

comparisons between this study and other studies so challenging. Although several reviews have been published (Hintz, 1969; Olsson, 1969; Parra, 1978) drawing comparisons between the digestive capabilities of foregut and hindgut fermenters, they were limited by the previously described variables. However, the reviewers suggested that the fiber digesting capabilities of nonruminant herbivores are commonly less than those of ruminants.

Generally speaking, animals with a larger body mass consume a smaller percentage of their body weight on a daily basis because their mass-specific energy requirements (kcal/kg) decrease with increasing body size (Van Soest, 1982). The level of consumption also is a function of the caloric density of the diet.

***Varecia variegata* spp.**

Surprisingly, very little information could be located in the literature concerning the natural feeding habits or gastrointestinal anatomy of either black and white or red ruffed lemurs (Tattersall, 1982). Additionally, no previous measurements or estimates of dry matter intake by *Varecia variegata* spp. were available. Petter et al. (1977) described *Varecia* as frugivorous, a feeding strategy that Tattersall (1982) suggested is in agreement with inferences from their dental morphology.

Recent studies of *Varecia* sp. in their native habitat indicate that these animals utilize fruits and nectar as 70.8% and 15.3% of their total food resources, respectively (White, 1991). Leaves (11.1%), undesignated as to maturity, and flowers (2.8%) make up the remaining portions of the diet. The author noted that the flowers were licked but not consumed, suggesting their use as a source of pollen and/or nectar. Although the majority (86.1%) of the diet appeared to consist of what would be considered "more digestible" food items, there was no chemical analysis to support this assumption.

Food items selected by a captive group of black and white ruffed lemurs were described in a study of species behavior by Pereira et al. (1988). As with the previously mentioned study, no attempt was made to quantify food items selected. The author did indicate that the animals consumed leaves, grasses, buds, flowers, and acorns (*Quercus* spp.). However, there was no suggestion that this diet was comparable to that selected by animals in their native habitat.

The digestive capabilities of *Varecia variegata* ssp. have been a subject of curiosity among many who have cared for this species in captivity. When fed a mixed diet similar to those described in previous studies, food items such as yams, carrots, and apples appear in the feces in a physical form similar to that which was offered (e.g., cubed, sliced). From

these observations, an assumption has been made that these animals utilize very little, if any of these foods and raises questions concerning the ability of this species to digest other foods as well. This assumption seems to be supported by the relatively low dry matter digestibilities seen in this study (51.0% of 15ADF and 41.7% of 30ADF). The reduced dry matter digestibility of 30ADF is a further representation that this species lacks specific gastrointestinal adaptations for utilization of a fibrous diet.

The significant reduction in body weight of *Varecia variegata* ssp. when consuming diet 30ADF also was indicative of the limited ability of this species to use a diet with elevated levels of plant cell wall. Although dry matter intakes increased significantly, there was a concurrent reduction in digestibility of dry matter. Since food was always provided *ad libitum*, it appears that the 30ADF diet alone was not suitable to support the caloric requirements of *Varecia variegata* spp.

Ruffed lemurs have demonstrated a coprophagic behavior in captivity (Edwards, personal observation), although the animals were not permitted access to their feces during these trials. This type of nutrient recycling may permit the ruffed lemur to recover some of the undigested nutrients lost in the fecal matter.

Another common observation concerning *Varecia* spp. in

captivity is the apparent rapid rates of digesta transit. As one keeper noted, "you can return 20 min after feeding the animals, and find the food you just offered in the feces". In fact, some have questioned whether the material was fecal in origin or regurgitated food, due to the similar physical characteristics and rapid appearance. Although the first fecal collection was conducted at 3 h post ingestion of the dietary marker, visual observations made during the collection period suggest that transit time (TT_1) is more rapid (<1 h) than the 3.0 h reported here.

Although there were no statistically significant differences between the estimates of DE for 15ADF and 30ADF for *Varecia*, the animals fed 30ADF consumed more dry matter (5.49% BW) than those fed 15ADF (2.90% BW). This presumably was a metabolically driven attempt to maintain caloric intake. However, this strategy appears not to have been effective since there was a significant reduction in mean body mass (4.68 kg vs. 4.04 kg) while consuming 30ADF. These animals were simply unable to digest and absorb adequate calories to maintain their body mass.

The above observations all suggest that lemurs lack gastrointestinal adaptations that permit the retention of digesta for a time sufficient to allow microbial fermentation of plant cell wall. Even so, this species selects a natural diet entirely of plant origin. Similar digestive patterns

and dietary habits have been observed in another herbivore of comparable body size, the red panda (*Ailurus fulgens*) (Table 3-21).

Table 3-21. Digestible energy (DE) and dry matter intake (DMI) of two nonspecialized herbivores of similar body weight.

Species	Diet	DE (kcal/g DM)	DMI (g/kg BW)
<i>Varecia variegata</i>	15ADF	2.20	29.0
<i>Varecia variegata</i>	30ADF	2.74	54.9
<i>Ailurus fulgens</i> ^a	G/alf ^b	3.14	28.6
<i>Ailurus fulgens</i> ^a	G/bam ^c	3.69	27.0

^aWarnell (1988).

^bGruel mixture with 10% alfalfa meal.

^cGruel mixture with 10% bamboo (*Psuedosasa japonica*) meal.

The high rate of digesta passage suggests that limited digestion of insoluble plant material requires an increased turnover of ingesta (Table 3-22). This is reflected in the

Table 3-22. Transit time (TT₁, h) and total mean retention time (R_{git}, h) of particulate markers for two nonspecialized herbivores of similar body weight.

Species	Diet	TT ₁	R _{git}
<i>Varecia variegata</i>	15ADF	3.0	5.2
<i>Varecia variegata</i>	30ADF	2.5	4.9
<i>Ailurus fulgens</i> ^a	Bamboo	5.0	5.7
<i>Ailurus fulgens</i> ^a	G/alf ^b	5.2	9.6
<i>Ailurus fulgens</i> ^a	G/bam ^c	6.1	13.3

^aWarnell (1988).

^bGruel mixture with 10% alfalfa meal.

^cGruel mixture with 10% bamboo (*Psuedosasa japonica*) meal.

slower rates of transit and longer retention in the red pandas fed bamboo versus a forage/concentrate mixed diet. With lower gross energy digestibilities (DE), *Varecia* spp. have adapted by attempting to fulfill their energy needs by exposing a large mass of food to digestive processes per unit of time and by rapidly passing the undigested portion.

Rapid rates of transit and reduced capacities for fiber digestion indicate that a substantial portion of the diet selected by free-ranging ruffed lemurs would be passed in the fecal material. This feeding/digestive strategy would be an ideal method of seed dispersal for many of the fruits consumed by this species, presuming the seed coat can withstand the limited digestive assault demonstrated in this study.

Strict adherence to descriptions of the five classes or degrees of herbivory in primates (Eisenberg, 1978) (see Chapter I) would place *Varecia variegata* spp. in Class 1, based upon their "apparent lack of digestive tract modification". Yet the dietary habits of primates in this class (omnivorous feeding strategies) do not correspond with current information on the natural dietary habits of ruffed lemurs. Therefore, if *Varecia* spp. are classified according to a specific degree of herbivory, this species appears to fit the description of Class 2 more appropriately. Future descriptions of the gastrointestinal anatomy of *Varecia* spp. will help to clarify this issue.

***Alouatta* spp.**

Members of the genus *Alouatta* have been described as "behavioral folivores" suggesting that howlers, lacking the extensive gastrointestinal adaptations of the Old World folivores, select foods perceived as more readily digestible (e.g., young leaves and fruits). Although this description may apply to a particular species as it behaves in a specific region (i.e., *Alouatta palliata* on Barro Colorado Island; Milton, 1978), the description may be too broad to encompass the entire genus.

The digestibilities of NDF by the three species of *Alouatta* examined in this study were higher than those reported by Milton et al. (1980) (Table 3-23). The differences between studies may be explained by the dramatic differences in diet types and fiber sources tested, as well as by differences in methodology. One would predict that a diet composed of foliage and fruits, both containing unprocessed or "long-stem" fiber would be lower in digestibility than the extruded test diets, which consist of "processed" fiber particles.

The presence of a voluminous, complex large intestine is presumed to have evolved before the adaptations for foregut fermentation exhibited by the Old World colobines. The results of this study demonstrate that howler monkeys possess the capability of digesting and utilizing fibrous feeds, but

Table 3-23. Apparent digestibility (%) of plant cell wall (NDF), hemicellulose (HC), and cellulose (C) by howler monkeys (*Alouatta* spp.).

Species	Diet	NDF	HC	C
<i>A. caraya</i>	15ADF	46.5	53.6	38.0
	30ADF	45.8	63.6	36.8
<i>A. seniculus</i>	15ADF	43.4	43.8	40.8
	30ADF	44.8	56.4	37.3
<i>A. palliata</i>	15ADF	43.7	51.8	39.5
	30ADF	44.8	56.4	37.3
<i>A. palliata</i> ^a	Fruit ^b	23	18	29
	Leaf ^c	41	63	67

^aMilton et al. (1980).

^bFruit diet consisted of 81% ripe fig fruit from *Ficus yoponensis*, and *F. insipidia*, and 19% flush leaves from *Cecropia insignis*.

^cLeaf diet consisted of 87% young leaves from *Ficus insipida* and, *Cecropia insignis*, and 13% immature fruits from *Cecropia insignis* and *C. octusifolia*.

the ADMD of diets 15ADF and 30ADF represent only 85.3% and 80.5%, respectively, of the same values measured in colobines.

Comparable differences have been reported (Udén, 1978) for other hindgut and foregut fermenters fed similar diets. Horses digested 85.8% as much DM as goats, and ponies digested 81.0% as much DM as heifers.

The significant reduction (11%) in ADMD seen in howlers fed diet 30ADF versus 15ADF supports the relatively lower ability of a hindgut fermenter to utilize a higher fiber food. The colobine species exhibited only a 5.7% reduction in ADMD when comparing diets 30ADF and 15ADF.

Howler monkeys digested relatively more of the hemicellulose fraction of both diets 15ADF and 30ADF than the cellulose fraction as compared to digestion of those components by the foregut fermenters. This has been observed in hemicellulose digestion by domestic hindgut fermenters (equids) versus foregut fermenters (cattle, sheep, goats) as well (Van Soest, 1994). Although there is no single explanation for this, there has been speculation that xylan cannot be processed by microorganisms until the arabinosic side chains are removed. Another view is that the digestion of xylan is dependent upon the removal of cellulose that surrounds it. It is possible that some linkages which are sensitive to gastric digestion, must be removed from the xylan to allow further digestion, which in this case would occur in the hindgut. Finally, it is thought that some hemicellulosic carbohydrates may exist as glycoproteins that are released by the action of acid pepsin. Apparent digestibilities of cellulose and hemicellulose for three species of howlers are compared to values determined in other hindgut fermenters in Table 3-24.

In general, it is believed that nonruminant herbivores have shorter retention times than ruminants. These trends were not consistently exhibited in this study. Estimates of digesta transit reported here are comparable with two previous studies examining these parameters in *Alouatta* sp. (Milton,

Table 3-24. Digestibility (%) of cellulose (C) and hemicellulose (HC) by various nonruminant animals.

Species	Diet	C	HC	Author
<i>Alouatta caraya</i>	15ADF	38.0	53.6	Current study
	30ADF	36.8	63.6	Current study
<i>Alouatta villosa palliata</i>	15ADF	39.5	51.8	Current study
	30ADF	44.5	66.8	Current study
<i>Alouatta seniculus sara</i>	15ADF	40.8	43.8	Current study
	30ADF	37.3	56.4	Current study
Elephant, Asian	Alfalfa	56	49-68	Foose, 1982
	Timothy	45-57	52-54	Foose, 1982
Elephant, African	Alfalfa	44-62	69-75	Foose, 1982
	Timothy	42-46	38-49	Foose, 1982
Horse, pony	Timothy	37	38-45	Udén, 1978
	Timothy	37-42	38-45	Foose, 1982
Zebra, mountain	Alfalfa	54-64	36-48	Foose, 1982
	Timothy	38-43	47	Foose, 1982
Tapir, Asian	Alfalfa	33-35	10-27	Foose, 1982
	Timothy	29-47	36-57	Foose, 1982

1981; Crissey et al., 1989). Although not statistically significant, TT_1 was more rapid for Co-EDTA and slower for Cr-mordanted fiber when the howlers were fed 15ADF than when fed 30ADF. With acetate beads, TT_1 with values determined on diet 30ADF were more rapid than those for 15ADF and R_{git} values were shorter. The only other R_{git} determined with howlers and reported in the literature (134 h) (Crissey et al., 1989) was significantly longer than those reported in this study (24.2-38.8 h). Although the diets used in these two studies were comparable in composition, the types of markers used were not similar and this may account, in part, for the differences between the studies.

It appears that the three species of *Alouatta* studied exhibited all of the criteria proposed by Eisenberg (1978) for classifying howlers as Class 4 herbivores, having both the gastrointestinal tract modifications and natural diets containing at least 40% leaves. This classification also is supported by the results presented in Chapter II. If one were to apply Hoffman's (1973) classification of herbivores, the howler might be considered an intermediate feeder, exhibiting the ability to shift from leaf material to plant parts that are relatively more digestible as a function of seasonal availability.

Colobines (*Colobus*, *Pygathrix*, *Trachypithecus*)

One of the important characteristics of herbivores is an increased capacity for temporary retention of food in the gastrointestinal tract, when compared to omnivorous or carnivorous species (Parra, 1978). The fermentation contents (digesta in the rumen or saccus + cecum + colon) expressed as a percentage of BW, of langurs and other herbivores with foregut fermentation are compared in Table 3-25.

Table 3-25. Fermentation contents (FC) (rumen or saccus + cecum + colon) of species with foregut fermentation, expressed as a percentage of BW (Parra, 1978).

Species	FC (%BW)	Author
Langur	13.0	Kuhn (1964)
Langur	17.4	Bauchop and Martucci (1968)
Sheep	10.1	Elsden et al. (1946)
Sheep	15.6	Boyne et al. (1956)
Cattle	10.0	Nevens (1928)
Cattle	17.8	Elsden et al. (1946)
Eland	11.9	Hungate et al. (1959)
Camel	12.3	Hungate et al. (1959)

Dry matter intakes of both diets 15ADF and 30ADF, 1.42% and 1.44% of body weight, respectively, seen in *Colobus guereza* in this study were lower than those reported by both Oftedal et al. (1982), 1.8%, and Watkins et al. (1985), 1.99%. Watkins et al. (1985) suggested that the elevated levels of

consumption of the test diet in their study were a function of the higher (25% versus 16%) cell wall (NDF) content of the test diet. However, one would predict that intake levels of 15ADF (24% NDF) in this study would be similar to those reported by Watkins et al. (1985). The absolute dry matter intakes, 154.8g/d of 15ADF and 153.8g/d of 30ADF, which were not statistically different between the two dietary treatments, are similar to those reported in other studies with colobus (159 g/d; Oftedal et al., 1982; and 158 g/d; Watkins et al., 1985). Variations seen between the three studies may be a result of the differences in composition of the test diets, differences in their caloric densities, and differences in the body weights and body compositions of study subjects.

Dierenfeld et al. (1992) found that mean dry matter consumption of an individual proboscis monkey in a group of male and female animals fed a mixed ingredient diet was 3% of estimated body mass. The group of foregut fermenters involved in this study (*Colobus*, *Trachypithecus*, *Pygathrix*) consumed comparable levels of dry matter as a percentage of body weight (2.97% of 15ADF, 2.86% of 30ADF) with no significant differences between dietary treatments.

The single douc langur, which was the heaviest animal ($\bar{x}$ = 11.9 kg) included in the study, had the highest level of dry matter intake as a function of body weight (3.55% 15ADF, 3.33%

30ADF). This species is also the closest in body size to the proboscis monkey. However, Chivers (1994) indicated that the gastrointestinal tracts of these two species may be different. The gastrointestinal tract of the douc langur was described as the heaviest and most voluminous, relative to the other colobines examined by Chivers (1994). The proboscis monkey had only average volume. Although the proboscis had a very high functional absorptive area (FAA), the potential fermenting volume was low (Table 3-26).

Plant cell wall is also important as a primary restrictive determinant of intake (Van Soest, 1982). This is due in part to its effect on gut fill. However, the intake of forages and other fibrous feeds can be increased through the reduction of particle size by grinding and/or pelleting.

Dry matter digestibilities of 88 and 89% were calculated by Dierenfeld et al. (1992) for proboscis monkeys fed a mixed-ingredient diet during summer and winter trials, respectively. Although these digestibility estimates appear unusually high, Ullrey et al. (1982) also reported dry matter digestibilities as high as 90% in silvered leaf monkeys fed a mixed diet without browse plant supplementation. This higher level of dry matter digestibility appears to be related to the presence of readily fermentable and highly digestible foods (e.g., Zu·Preem Primate biscuits, fruits, lettuce) in the diets offered during the collection periods.

Table 3-26. Features of gut dimensions in colobine monkeys^a (Chivers, 1994).

Species	Gut length		Gut weight		Absorptive area ^b		Fermenting volume ^c		CGD ^d			
	GL	GL/BL	GW	%BW	AA	% of total	AA/BL	FV	% of total	Area	Wgt	Vol
<i>Colobus guereza</i>	483	7.8	363	5.8	2175	68	41	3332	92	392	2.1	2.7 12
<i>S. entellus</i>	445	7.0			2650	68	41	4473	90	447	1.7	9.3
<i>T. vetulus</i>	334	6.2			1650	64	31	2977	95		2.6	17
<i>T. cristatus</i>	540	10.4	372	6.1	2770	71	53	4023	89	660	1.4	4.9 8.1
<i>T. obscurus</i>	472	9.3	278	4.8	2460	70	48	3192	87	550	1.5	3.9 7
<i>Presbytis melalophos</i>	547	11.2	256	3.9	2477	73	51	2715	86	418	1.2	2.5 6
<i>Presbytis rubicunda</i>	548	10.5	229	4.4	2343	75	45	2598	86	499	1	3.6 6
<i>Pygathrix nemaeus</i>	526	9.2	276	6.7	2613	71	46	3575	88	872	1.4	4 7.3
<i>Nasalis larvatus</i>	886	13.8	598	3.8	4776	74	75	7244	87	456	1.1	2.9 6.4

^aGL=gut length, cm; BL=body length, cm; GW=gut weight, g; BW=body weight; AA=absorptive area, cm²;

FV=fermenting volume, cm³

^bArea of small intestine+1/2(stomach+cecum+colon), cm².

^cVolume of stomach+cecum+colon, cm³.

^d(Stomach+cecum+colon)/small intestine.

Sakaguchi et al. (1991) found the dry matter digestibility of a manufactured ("cubed") diet (16.4% ADF, DMB) fed to silvered leaf monkeys (*Semnopithecus crisatus*) was 75.7%. This value is lower, but comparable to the results of this project. Francois' langurs, a closely related species, digested 82.4% of the dry matter in diet 15ADF. The douc langur included in this study exhibited dry matter digestibilities of 76.2% and 73.9%, for diets 15ADF and 30ADF, respectively. These values were consistently lower than for other colobines (*Colobus*, *Trachypithecus*) in this study maintained on the same diets. Additionally, these values were the lowest apparent dry matter digestibility estimates reported for a colobine primate. Dry matter digestibility can be affected by the level of intake during the collection period (Church, 1988).

The significantly lower ADMD of diet 30ADF by all foregut fermenters (*Colobus*, *Pygathrix*, *Trachypithecus*) studied suggests that the elevated fiber concentrations in this diet provided a digestive challenge to these species. ADMD of mixed diets, including those containing browse plants, were not dramatically lower than those seen in this study.

Fiber component digestibility exhibited by the colobines demonstrates that these species are suited to consume a diet containing higher concentrations of plant cell wall. The lack of any significant differences in fiber digestibility between

the two diets further supports these findings. There were slight numerical differences between fiber digestibilities of the two diets, with digestibilities of NDF, ADF, and C in diet 30ADF of 96.9%, 89.5%, and 93.5%, respectively, of those digestibilities in diet 15ADF. Interestingly, as seen in the hindgut fermenting howlers, hemicellulose digestibility was numerically higher in diet 30ADF (77.0%) than in diet 15ADF (71.9%).

Similar, but numerically lower digestibilities of fiber by proboscis monkeys fed a mixed ingredient diet were as follows: 86.2-86.4% NDF, 87.1-90.4% HC, 85.0-86.0% ADF, 87.8-89.1% C, and 81.7-82.3% ADL (Dierenfeld et al., 1992.). These results support Chivers (1994) description of the proboscis monkey, the largest colobine included in his study, possessing the smallest stomach and largest large intestine. He indicated that this anatomical arrangement results in a low fermenting ability and high absorbing capability. This is further supported by natural dietary information indicating that this species eats few mature leaves (<50%), but selects fruit and young leaf parts (Yeager, 1989). Additionally, seed consumption approaches 20% in free-ranging proboscis. The extent of microbial fermentation which results from contributions of the hindgut in the proboscis was not examined.

Herbivores with foregut fermentation are more efficient

in their ability to digest plant fiber due to their adaptations to: consume large quantities of plant material, retain it for longer periods of time, and provide the environment required to support microbial digestive processes (Stevens, 1982). Table 3-27 includes dry matter and NDF digestibility estimates for three species of colobines included in this study compared to values determined for other species with foregut fermentation. The digestible energy estimates reported by Ullrey et al. (1982) are comparable to those seen in this study, when the differences in test diet are considered. Digestible energy was not determined by any other authors.

Bauchop and Martucci (1968) estimated the daily energy produced from microbial fermentation of ingesta in the foregut of an Asian colobine using the following assumptions. The stomach contents average 12% of body weight, and contents are, on average, 15% dry matter. The dry matter in the stomach contents of a 4.5-kg langur would be equivalent to 81 g. The quantified VFA molar composition of acetic:propionic:butyric:valeric acids was 56:24:13:7, and the average measured rate of fermentation per h was 460 $\mu\text{mole/g}$ of dry matter. They estimated that this would result in a daily energy equivalent of 283 kcal based upon the heat of combustion of each fatty acid. Using Klieber's (1961) interspecific value ($\text{BMR} = 70\text{BW}_{\text{kg}}^{0.75}$), the basal energy

Table 3-27. Digestibility (%) of dry matter and neutral-detergent fiber (NDF) by species with foregut fermentation.

Species	Diet	DM	NDF	Author
<i>Colobus guereza kikuyuensis</i>	15ADF	80.3	77.0	Current study
	30ADF	78.7	74.3	Current study
<i>Pygathrix nemaeus nemaeus</i>	15ADF	76.2	66.5	Current study
	30ADF	73.9	69.8	Current study
<i>Trachypithecus f. francoisi</i>	15ADF	82.4	79.3	Current study
	30ADF	76.7	75.7	Current study
Barasingha	Alfalfa	72.7	60.9	Foose, 1982
Eland	Timothy	56.4	54.9	Foose, 1982
	Alfalfa	60.2	39.8	Foose, 1982
	Timothy	52.9	49.8	Foose, 1982
Llama-guanaco	Alfalfa	71.5	69.4	Hintz et al., 1973
Cattle	Alfalfa	70.3	64.5	Foose, 1982
	Timothy	54.6	54.2	Foose, 1982
Sheep	Alfalfa	63.8	58.5	Hintz et al., 1973

requirement for a 4.5-kg langur would be 216 kcal per day. This latter value is 76% of Bauchop and Martucci's (1968) estimate of energy yield from microbial fermentation.

When the same assumptions used to calculate the above values are applied to the colobine primates involved in this study, 61 to 79% of the energy yield of microbial fermentation would be required for basal metabolic needs. The remainder presumably would be available toward support of the total maintenance requirement. These values are shown in Table 3-28.

The rate of digesta passage in small ruminants is expected to be more rapid than that of larger ruminants to support the animal's elevated energy demands, as a function of metabolic body weight ($BW^{0.75}$). One would predict a similar trend when comparing different species of colobines. Rates of passage (TT_1) determined with colobines in this study were slightly longer than those reported in two other studies (Sakaguchi et al., 1991; Dierenfeld et al., 1992). Based upon acetate bead marker recoveries of 96, 88, and 52% from proboscis monkeys fed a mixed ingredient diet, Dierenfeld et al. (1992) found a TT_1 of 14 h and a R_{GIT} of 49 h. This suggests that the proboscis monkey, when fed a mixed-ingredient diet has a TT_1 nearly twice as rapid as other colobines fed a higher fiber diet.

Results comparable to those determined with Francois'

Table 3-28. Body weight (BW), estimated daily energy production from microbial fermentation (MFE) of digesta based upon calculations by Bauchop and Martucci (1968), estimated basal metabolic rate (BMR) and percent of MFE used for BMR by colobines.

Species	ID	BW (kg)	MFE (kcal/d)	BMR (kcal/d)	BMR/MFE (%)
<i>Trachypithecus cristatus</i>	NA ^a	4.50	283	216	76
<i>Colobus guereza kikuyuensis</i>	Flower	11.34	713	433	61
	Gomez	10.90	685	420	61
<i>Pygathrix nemaeus nemaeus</i>	Rhett	12.10	761	454	60
<i>Trachypithecus f. francoisi</i>	Jack	7.71	485	324	67
	Janet	5.67	357	257	72
	Chrissie	6.67	419	291	69
	Stanley	3.99	251	198	79
	Fungar	5.75	362	260	72
	Goonqoot	5.85	368	263	71

^aData from Bauchop and Martucci (1968).

langurs are reported with silvered leaf monkeys fed a higher fiber "cubed" diet using like markers (Table 3-29). The rates of passage (TT_1) determined with Cr-mordanted fiber were slower and retention times (R_{git}) shorter in this species when compared to the silvered leaf monkey.

Table 3-29. Rates of digesta passage (TT_1 , h) and mean retention time (R_{git} , h) determined in two langur species fed similar higher fiber (15% ADF) diets.

Species	Marker type	TT_1	R_{git}
Silvered leaf monkey ^a	Cr	13.6	46.8
Silvered leaf monkey ^a	Co	13.6	44.8
Francois' langur	Cr	27.0	30.5
Francois' langur	Co	13.5	41.1

^aSakaguchi et al. (1991).

The anatomical and physiologic adaptations that permit colobines to support microbial fermentation of plant fiber and to utilize the end-products of that fermentation limit their ability to adapt to more digestible diets. The VFAs produced as a principle end-product of the fermentation process have a pK_a of 4.8. The symbiotic microorganisms responsible for VFA production cannot survive at a pH below 5.5 (Stevens, 1982). The pH of the colobine saccus contents is thought to be maintained in a manner similar to that of the rumen contents, i.e., by rapid absorption of VFAs and secretion of HCO_3 as a buffer by the salivary glands, pancreas, and other digestive

tract cells. The extent to which these mechanisms are present in the colobine saccus has yet to be determined (Kay and Davies, 1994).

If a colobine primate consumes excessive amounts of simple or readily fermentable carbohydrates (starch, sugar), the result would include rapid formation of VFAs in the foregut. This rapid production of VFAs in ruminants produces a dramatic drop in the pH of the digesta, increased absorption of VFAs, and replacement of the normal microbial organisms with lactobacilli. Lactobacilli produce lactic acid that may result in formation of hypertonic digesta, pulling water into the rumen and producing systemic dehydration. D-lactic acid produced in the forestomach is absorbed into the bloodstream, where it is only slowly metabolized, and leads to a systemic acidosis. Some of these changes have been observed in colobines receiving a concentrate-type diet (Bauchop and Martucci, 1968) or selecting a diet high in seeds (Ohwaki et al., 1974).

This rapid production of VFAs can produce necrosis and ulceration of the rumen epithelium, rumen immotility, and systemic acidosis, all of which are signs commonly observed in captive colobines (Janssen, 1994). Additionally, acute acidosis causes proliferation of coliforms and clostridial species that may produce enterotoxins and contribute to diarrhea (Church, 1988).

Eisenberg's (1978) categorizations of primate herbivory (Chapter I) would place both African and Asian colobines in Class 5, species that are close to being "obligate" folivores. Certainly, within such a broad grouping, there will be variability. As with *Alouatta*, there is strong evidence from field data that some colobines may utilize plant parts that are relatively more digestible when they are seasonally available.

Markers

Markers may be used to measure the movement of digesta through the gastrointestinal tract as well as indirect indicators of food digestibility. Those markers used for the purpose of estimating digestibility are typically fed or administered at a constant level in the diet (Van Soest et al., 1983). Acid-detergent lignin has been used as an internal indicator of food digestibility (Van Dyne, 1968; Ullrey et al., 1987). Application of this method assumes that the lignin fraction of the diet is totally indigestible by the host and the gastrointestinal microflora. Van Dyne (1968) stated that the apparent digestibility (AD) of nutrients may be determined, using the following lignin-ratio technique:

$$AD = 100 - \frac{(\% \text{ Nutrient in feces}) (\% \text{ Lignin in ingesta})}{(\% \text{ Nutrient in ingesta}) (\% \text{ Lignin in feces})}$$

The primary limitations of this method lie in the assumption of lignin indigestibility and the analytical error involved in lignin determination. These limitations of lignin analysis are well documented (Van Soest, 1994). To use lignin as a marker for estimates of food or nutrient digestibility, it has been stated that the dietary lignin concentration should be at least 6.0% (Van Soest, 1995).

Relatively high apparent digestibility of acid detergent lignin was observed in this study (39.7-68.9%). Similar results were reported in feeding trials with black and white colobus (Watkins et al., 1985; Oftedal et al., 1982). These values appear to originate from a combination of low lignin concentrations (< 2%) in the test diets used in these trials and the analytical errors involved in lignin determination previously described.

Particulate Markers

Concerns surrounding the application of particulate markers, such as acetate beads, seeds, and glass balls, have been expressed by several authors. The primary argument against these markers is their potential to traverse the gastrointestinal tract in a manner different from the digesta. Some of this deviation from natural movement is a result of differences in specific gravity. Suitable markers should behave as part of the digesta the investigator wishes to mark,

without producing other effects. However, the suitability of a marker is related, in part, to how it is used. For example, the acetate bead may be a suitable marker for solid phase digesta within species lacking a complex gastrointestinal tract. In animals with gastrointestinal sacculations and folds, acetate beads may become entrapped and separate from the remainder of the digesta. The type of food offered during the trial and the desired measurement (e.g., transit time) will dictate which marker may be successfully applied. Finally, the facilities and equipment available to analyze the excreted marker will influence the marker choice.

Inorganic Compounds

It has been demonstrated that liquid and particulate matter flow differently through the gastrointestinal tract. Large ungulates, ruminants, horses, and pigs tend to retain fiber (solid) relative to liquid while some rodents, and rabbits selectively retain liquid relative to fiber (solid).

The two inorganic markers most commonly used to measure these fractions, Cr-fiber (solid) and Co-EDTA (liquid), have been applied to numerous species. Comparative passage rates of liquid and solids in some animals, including the results of this study, are presented in Table 3-30. The lack of statistical differences between the rates determined for the two markers in this study appear to be a function of the

Table 3-30. Comparative passage rates of solid and liquid digesta in species with simple GIT, hindgut, and foregut fermentation (Udén, 1978; Van Soest et al., 1983).

Species	Diet type ^a	BW (kg)	Whole tract retention (R _{git})	
			Solid (h)	Liquid (h)
SIMPLE GIT				
Ruffed lemur	1	4.7	3.8	4.1
Ruffed lemur	2	4.0	2.3	2.4
Man	4	70	41	39
HINDGUT				
howler	1	7.5	38.8	34.1
howler	2	7.6	38.8	40.4
horse	3	388	21	17
pony	3	132	25	16
rabbit	3	3	5	193 ^b
FOREGUT				
colobine	1	7.5	37.6	41.1
colobine	2	7.5	68.6	38.4
cattle	3	243	48	20
sheep	3	30	57	26
goat	3	29	41	28

^a1=15ADF.

2=30ADF.

3=Timothy hay.

4=Standard diet including 20 g of dietary fiber from wheat bran.

^bProlonged retention results from selective retention of liquid as well as selective coprophagy of the less fibrous night feces.

sample size.

In general, there was an increase in passage rate (decreased retention) of both phases of digesta seen in ruffed lemurs when fed 30ADF as compared to 15ADF. This would

further support the previously described digestive strategies of these two subspecies.

The approximately equal retention times for solid and liquid digesta exhibited by howlers are similar to the relative rates R_{git} reported for other hindgut, noncoprophagic species. Species with foregut fermentation exhibit a more rapid passage of liquid than solid digesta. This is consistent with relative liquid and solid retention times (R_{git}) seen in colobines fed 30ADF; however, when fed 15ADF, the solid digesta R_{git} appears to be appreciably shorter.

CONCLUSION

The gastrointestinal and dietary adaptations that are well known in domestic herbivores also are seen in leaf-eating primates. Rapid rates of passage and reduced digesta retention are particularly evident in herbivorous species such as red ruffed lemurs and black and white ruffed lemurs that lack specific gastrointestinal tract modifications for microbial fermentation of plant fiber. This results in a reduced ability to digest ingested plant material and requires increased rates of intake. One would predict the time spent feeding by these species, as a percent of daily activity would be greater than that of other leaf-eating primates.

Increased retention times and reduced rates of passage are observed in leaf-eating primates with adaptations for

either hindgut or foregut fermentation. Digestive efficiencies of hindgut fermenters (mantled howler, red howler, and black howler) are significantly less than those of colobines. These reduced digestive efficiencies are comparable to those seen when contrasting horse and cattle and appear to be related to the lack of extensive gastrointestinal modifications anterior to the sites of gastric and enzymatic digestion. Hindgut fermenters also have a reduced absorptive surface area posterior to the site of microbial fermentation.

Colobine primates (black and white colobus, Francois' langur, douc langur) exhibit the most extensive gastrointestinal modifications for microbial fermentation of plant cell wall. Although there is a diversity of feeding habits among these species, foregut fermentation is present throughout the subfamily. As a result, regardless of the type of plant material consumed, that food is subjected to fermentative processes.

Primates with either hindgut or foregut fermentation subjected to thousands of years of evolutionary pressure, have developed mechanisms to accomodate readily available plant food and effectively degrade plant fiber, yielding a significant amounts of energy through symbiotic relationships with gut microorganisms. The unfortunate consequences of presenting rapidly fermentable foods to these primates are illustrated in much of the literature concerned with their

captive husbandry. The impression that plant fiber is a negative component in diets, and that a diet low in this fraction is "preferred" by these captive primates, has produced many of the health problems commonly seen.

It is apparent, from these and other studies that plant fiber should be considered with equal importance to "true" nutrients when formulating diets for herbivorous primates.

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APPENDIX A

Table A1. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Anacardiaceae						
<i>Mangifera indica</i>	(1)	YL	Wet	1	20.6	-
<i>Mangifera indica</i>	(2)	UF	Dry	4	22.5	0.00
<i>Mangifera indica</i>	(3)	UF	Wet	1	19.0	-
<i>Mangifera indica</i>	(4)	RF	Dry	3	22.1	2.09
<i>Mangifera indica</i>	(5)	PUL	Dry	2	31.8	0.48
Annonaceae						
<i>Annona jahnii</i>	(6)	L	Wet	1	28.3	-
<i>Annona jahnii</i>	(7)	UF	Wet	1	30.2	-
<i>Annona jahnii</i>	(8)	RF	Wet	1	27.2	-
<i>Annona jahnii</i>	(9)	FL	Wet	1	19.1	-
<i>Annona punicifolia</i>	(10)	UF	Wet	1	16.0	-
<i>Annona punicifolia</i>	(11)	RF	Wet	3	36.8	25.90
Arecaceae						
<i>Copernicia tectorum</i>	(12)	F	Wet	2	28.2	2.90
<i>Copernicia tectorum</i>	(13)	UF	Dry	3	33.1	3.45
<i>Copernicia tectorum</i>	(14)	UF	Wet	1	ND	-
<i>Copernicia tectorum</i>	(15)	RF	Wet	1	27.8	-

Table A1 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Anacardiaceae								
(1)	14.9	-	3.1	-	4.4	-	4.58	-
(2)	2.5	0.12	1.5	0.14	2.9	0.07	4.05	0.05
(3)	2.5	-	1.2	-	2.5	-	4.02	-
(4)	4.5	1.05	1.6	0.22	2.8	0.62	4.24	0.07
(5)	2.6	0.08	2.5	0.31	11.0	0.18	4.06	0.12
Annonaceae								
(6)	17.8	-	3.2	-	7.3	-	5.03	-
(7)	10.1	-	10.7	-	4.5	-	5.06	-
(8)	14.7	-	12.5	-	4.0	-	5.35	-
(9)	17.5	-	6.9	-	5.9	-	5.22	-
(10)	10.8	-	3.6	-	3.4	-	4.80	-
(11)	9.7	0.45	13.3	1.00	3.2	0.28	5.15	0.16
Arecaceae								
(12)	6.7	0.21	3.7	3.36	8.0	0.08	4.53	0.33
(13)	7.2	0.01	0.5	0.35	8.0	0.29	4.58	0.05
(14)	6.0	-	0.6	-	8.5	-	4.61	-
(15)	5.0	-	0.7	-	6.3	-	4.33	-

Table A1 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Anacardiaceae								
(1)	37.0	-	14.1	-	3.3	-	10.7	-
(2)	55.7	2.09	8.0	0.26	1.5	0.18	6.2	0.33
(3)	15.8	-	9.3	-	4.5	-	5.0	-
(4)	15.9	4.01	13.5	4.24	7.9	2.82	5.8	1.06
(5)	38.3	1.80	29.0	1.16	9.5	0.60	19.3	1.23
Annonaceae								
(6)	57.5	-	37.4	-	13.9	-	22.7	-
(7)	67.9	-	46.9	-	30	-	16.7	-
(8)	59.0	-	41.5	-	15.8	-	25.7	-
(9)	57.5	-	45.8	-	24.7	-	20.8	-
(10)	69.8	-	52.1	-	23.5	-	28.2	-
(11)	52.1	1.40	39.4	2.14	19.5	4.11	21.4	5.14
Arecaceae								
(12)	70.2	12.49	50.8	17.33	32.8	14.41	17.9	2.97
(13)	80.8	1.93	45.9	1.42	23.2	1.11	22.6	0.31
(14)	68.3	-	33.2	-	16.6	-	16.5	-
(15)	55.7	-	35.5	-	20.4	-	14.9	-

* L= mature leaf; NL= new leaf; YL= young leaf; F= fruit; UF= unripe fruit; RF= ripe fruit; FL= flower; PET= petiole; PUL= pulvinus

Table A2. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Asclepidaceae						
<i>Marsdenia undulata</i>	(16)	L	Wet	3	33.4	21.84
<i>Marsdenia undulata</i>	(17)	UF	Wet	1	10.0	-
Bombacaceae						
<i>Ceiba pentandra</i>	(18)	FLBU	Dry	1	20.2	-
Cactaceae						
<i>Pereskia guamacho</i>	(19)	RF	Wet	1	25.3	-
Chrysobalanaceae						
<i>Licania pyrifolia</i>	(20)	FL/BU	Wet	1	30.6	-
<i>Licania pyrifolia</i>	(21)	NL	Dry	1	23.9	-
<i>Licania pyrifolia</i>	(22)	L	Dry	2	40.8	0.50
Cucurbitaceae						
<i>Melothria trilobata</i>	(23)	L	Wet	2	17.2	0.08
Dilleniaceae						
<i>Tetracera volubris</i>	(24)	FL	Wet	1	22.8	-
Euphorbiaceae						
<i>Sapium aucuparium</i>	(25)	L	Wet	3	67.0	2.41

Table A2 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Asclepidaceae								
(16)	12.6	2.00	6.2	0.20	9.2	0.43	4.61	0.07
(17)	5.7	-	5.0	-	3.3	-	4.30	-
Bombaceae								
(18)	13.0	-	1.3	-	8.2	-	4.36	-
Cactaceae								
(19)	9.1	-	2.4	-	4.1	-	4.39	-
Chrysobalanaceae								
(20)	9.6	-	2.4	-	3.6	-	4.99	-
(21)	19.2	-	2.5	-	5.8	-	4.96	-
(22)	9.9	0.39	5.2	0.23	3.9	0.11	4.48	0.54
Cucurbitaceae								
(23)	15.6	6.95	5.7	2.78	15.3	0.29	4.21	0.04
Dilleniaceae								
(24)	13.6	-	3.5	-	8.5	-	4.70	-
Euphorbiaceae								
(25)	15.1	0.08	6.3	0.40	14.0	0.10	4.31	0.11

Table A2 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Asclepidaceae								
(16)	50.1	4.81	33.3	5.49	12.9	3.41	20.2	1.85
(17)	28.3	-	20.3	-	6.2	-	14.7	-
Bombacaceae								
(18)	64.6	-	50.4	-	30.3	-	20.0	-
Cactaceae								
(19)	54.7	-	35.1	-	12.3	-	23.8	-
Chrysobalanaceae								
(20)	67.9	-	58.7	-	40.1	-	20.4	-
(21)	57.9	-	53.3	-	33.7	-	19.0	-
(22)	74.0	0.60	49.5	0.76	24.3	0.70	24.1	0.50
Cucurbitaceae								
(23)	43.0	4.84	38.5	2.48	14.5	1.74	20.5	1.06
Dilleniaceae								
(24)	62.5	-	53.2	-	40.1	-	20.4	-
Euphorbiaceae								
(25)	36.8	4.70	30.1	5.30	8.6	4.00	16.0	0.90

* L= mature leaf; NL= new leaf; YL= young leaf; F= fruit; UF= unripe fruit; RF= ripe fruit; FL= flower; PET= petiole; PUL= pulvinus

Table A3. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part*	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Caesalpinoideae)						
<i>Cassia grandis</i>	(26)	L	Wet	3	51.6	12.13
<i>Cassia grandis</i>	(27)	UF	Wet	3	10.3	1.63
<i>Cassia moschata</i>	(28)	L	Wet	5	45.8	4.06
<i>Cassia moschata</i>	(29)	L	Dry	1	48.3	-
<i>Cassia moschata</i>	(30)	YL	Wet	1	32.9	-
<i>Cassia moschata</i>	(31)	YL	Dry	2	36.7	2.88
<i>Cassia moschata</i>	(32)	UF	Wet	3	20.3	1.49
Fabaceae (Mimosoideae)						
<i>Albizia columbiana</i>	(33)	L	Wet	1	81.0	-
<i>Albizia guachapele</i>	(34)	L	Wet	2	35.4	-
<i>Albizia guachapele</i>	(35)	L	Dry	1	37.1	-
<i>Albizia guachapele</i>	(36)	YL	Wet	1	28.7	-
<i>Albizia guachapele</i>	(37)	NL	Wet	3	31.0	1.98
<i>Enterolobium cyclocarpum</i>	(38)	F	Wet	-	-	-
<i>Pithecellobium dualense</i>	(39)	L	Wet	5	45.3	2.21
<i>Pithecellobium dualense</i>	(40)	FL(BU)	Wet	2	22.2	0.74
<i>Pithecellobium saman</i>	(41)	L	Wet	7	38.3	7.44

Table A3 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(26)	12.5	0.26	4.7	2.67	6.3	1.08	5.19	0.11
(27)	10.6	1.63	0.8	0.40	8.3	0.25	4.62	0.26
(28)	12.1	1.62	5.3	1.57	5.2	0.99	5.17	0.24
(29)	14.8	-	5.1	-	6.8	-	4.82	-
(30)	12.8	-	1.5	-	3.0	-	5.39	-
(31)	16.6	0.81	1.2	0.12	3.5	0.11	5.03	0.03
(32)	7.1	1.66	1.5	0.32	3.6	0.29	4.76	0.29
Fabaceae								
(33)	18.8	-	8.3	-	4.0	-	5.69	-
(34)	26.4	1.81	4.4	0.14	4.5	0.32	5.06	0.04
(35)	22.3	-	5.4	-	4.3	-	5.10	-
(36)	25.3	-	1.9	-	4.2	-	4.89	-
(37)	33.0	2.76	2.7	0.25	4.4	0.24	5.17	0.24
(38)	-	-	-	-	-	-	-	-
(39)	16.9	0.80	3.2	0.53	3.7	0.18	5.49	0.25
(40)	27.7	0.08	1.4	0.94	5.4	0.09	5.19	0.17
(41)	23.2	2.38	7.0	2.38	3.1	0.44	5.61	0.11

Table A3 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(26)	50.5	4.13	39.3	3.51	20.2	3.69	17.6	1.87
(27)	21.8	1.90	34.0	3.31	19.9	3.57	9.1	0.94
(28)	56.3	6.43	40.9	8.64	22.0	7.71	17.3	1.26
(29)	53.6	-	45.0	-	21.1	-	22.1	-
(30)	65.0	-	46.7	-	29.4	-	18.5	-
(31)	54.1	5.13	38.4	7.99	19.2	10.43	13.3	1.59
(32)	46.2	16.42	38.6	7.48	15.4	4.88	22.6	10.23
Fabaceae								
(33)	70.9	-	50.0	-	33.2	-	15.0	-
(34)	55.7	8.40	33.6	1.83	17.5	1.19	15.9	3.03
(35)	55.4	-	33.4	-	15.3	-	18.2	-
(36)	72.3	-	40.2	-	20.8	-	19.2	-
(37)	49.7	10.56	23.5	1.59	11.3	1.70	11.5	0.83
(38)	-	-	-	-	-	-	-	-
(39)	74.6	3.95	49.9	5.59	31.5	4.68	18.6	1.17
(40)	44.2	2.81	16.8	0.52	7.4	0.49	9.2	0.31
(41)	59.4	4.54	41.6	3.85	22.3	3.70	18.8	6.36

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole;

Table A4. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Mimosoideae)						
<i>Pithecellobium saman</i>	(42)	L	Dry	2	36.9	1.07
<i>Pithecellobium saman</i>	(43)	NL	Dry	1	ND	-
<i>Pithecellobium saman</i>	(44)	YL	Wet	3	24.5	1.29
<i>Pithecellobium saman</i>	(45)	FLBU	Dry	1	ND	-
<i>Pithecellobium saman</i>	(46)	FL	Dry	2	19.0	1.78
<i>Pithecellobium saman</i>	(47)	RF	Dry	1	44.0	-
<i>Pithecellobium saman</i>	(48)	UF	Dry	2	22.5	-
<i>Pithecellobium tortum</i>	(49)	L	Wet	5	38.0	3.70
<i>Pithecellobium tortum</i>	(50)	YL	Wet	1	22.2	-
<i>Pithecellobium tortum</i>	(51)	FL	Wet	1	18.8	-
<i>Pithecellobium tortum</i>	(52)	LBU, NL	Dry	2	41.8	0.11
<i>Pithecellobium tortum</i>	(53)	UF	Dry	1	71.4	-
Fabaceae (Papilionoideae)						
<i>Entada polystachya</i>	(54)	L	Wet	1	43.7	-
<i>Machaerium moritzianum</i>	(55)	FL	Dry	1	ND	-
<i>Platymiscium diadelphum</i>	(56)	L	Wet	1	37.5	-
<i>Platymiscium diadelphum</i>	(57)	YL, NL	Wet	1	31.2	-

Table A4 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(42)	22.8	0.85	5.3	0.23	3.3	0.03	5.51	0.06
(43)	36.1	-	1.8	-	5.2	-	5.78	-
(44)	29.3	0.19	1.5	0.43	4.0	0.08	5.53	0.12
(45)	ND	-	2.8	-	ND	-	5.89	-
(46)	19.3	0.52	1.8	0.18	4.9	1.05	4.74	0.01
(47)	16.4	-	1.8	-	3.3	-	4.61	-
(48)	17.3	0.41	1.5	0.29	3.6	0.32	4.82	0.15
(49)	28.2	3.73	5.2	1.88	6.2	1.57	5.29	0.18
(50)	35.7	-	3.9	-	5.0	-	5.07	-
(51)	ND	-	2.2	-	ND	-	5.19	-
(52)	32.8	2.15	1.6	0.15	3.5	0.37	5.20	0.03
(53)	23.2	-	1.1	-	3.2	-	4.68	-
Fabaceae								
(54)	17.6	-	5.2	-	3.9	-	5.30	-
(55)	ND	-	2.1	-	ND	-	ND	-
(56)	16.6	-	2.7	-	5.6	-	5.11	-
(57)	22.8	-	1.4	-	5.5	-	4.82	-

Table A4 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(42)	61.1	1.05	41.9	1.42	23.9	0.40	17.4	0.87
(43)	57.3	-	55.6	-	40.0	-	13.3	-
(44)	49.5	3.85	30.2	3.84	15.8	1.84	14.7	2.26
(45)	68.2	-	59.6	-	40.8	-	17.4	-
(46)	48.5	1.22	34.4	4.14	15.2	0.45	19.2	3.38
(47)	36.6	-	24.9	-	10.8	-	13.0	-
(48)	44.6	6.16	35.8	0.64	17.6	0.99	17.7	0.76
(49)	55.3	6.26	31.3	2.45	14.6	1.70	14.8	0.88
(50)	54.1	-	19.5	-	8.5	-	10.8	-
(51)	44.6	-	20.7	-	8.0	-	13.0	-
(52)	48.2	6.28	34.9	3.65	18.2	1.48	15.6	4.71
(53)	48.0	-	31.4	-	9.3	-	21.0	-
Fabaceae								
(54)	64.4	-	45.9	-	14.5	-	30.4	-
(55)	61.9	-	33.2	-	18.7	-	17.6	-
(56)	57.9	-	39.7	-	19.7	-	20.4	-
(57)	43.7	-	23.6	-	12.6	-	11.1	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A5. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Papilionoideae) (Cont'd)						
<i>Platymiscium polystachyum</i>	(58)	YL	Wet	1	21.2	-
<i>Platymiscium polystachyum</i>	(59)	FLBU	Wet	1	17.9	-
<i>Pterocarpus acapulcensis</i>	(60)	L	Wet	4	33.3	8.49
<i>Pterocarpus acapulcensis</i>	(61)	NL	Wet	4	27.6	1.77
Moraceae						
<i>Ficus pertusa</i>	(62)	L	Dry	3	26.5	16.32
<i>Ficus pertusa</i>	(63)	L	Wet	4	29.6	3.17
<i>Ficus pertusa</i>	(64)	UF	Wet	2	23.1	0.28
<i>Ficus pertusa</i>	(65)	RF	Wet	3	22.8	1.09
<i>Ficus trigonata</i>	(66)	UF	Wet	1	16.3	-
Poyngonaceae						
<i>Coccoloba sp.</i>	(67)	YL	-	-	-	-
Rhamnaceae						
<i>Zizyphys saeri</i>	(68)	L	Wet	1	43.5	-
<i>Zizyphys saeri</i>	(69)	L	Dry	1	35.0	-
<i>Zizyphys saeri</i>	(70)	F	Wet	1	39.8	-

Table A5 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(58)	25.0	-	2.7	-	6.9	-	5.31	-
(59)	25.5	-	2.5	-	7.4	-	5.13	-
(60)	19.1	0.61	1.5	0.37	4.8	0.05	5.09	0.23
(61)	24.9	5.23	1.2	0.04	4.3	0.23	5.13	0.14
Moraceae								
(62)	11.2	5.02	2.7	0.85	9.6	0.20	4.29	0.03
(63)	12.3	1.47	3.9	0.45	11.4	1.43	4.23	0.15
(64)	7.1	0.17	2.0	0.41	6.9	0.17	4.89	0.04
(65)	4.9	0.26	3.3	1.39	4.9	0.36	4.50	0.02
(66)	10.5	-	1.8	-	5.9	-	4.43	-
Polygonaceae								
(67)	-	-	-	-	-	-	-	-
Rhamnaceae								
(68)	14.1	-	2.2	-	10.6	-	4.51	-
(69)	22.6	-	1.6	-	8.6	-	4.59	-
(70)	5.9	-	0.8	-	6.1	-	4.59	-

Table A5 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (t)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae								
(58)	43.3	-	23.4	-	12.7	-	11.3	-
(59)	38.8	-	24.5	-	9.6	-	15.4	-
(60)	57.2	5.64	36.1	4.08	16.3	3.58	19.0	0.67
(61)	54.6	2.46	23.6	3.69	6.5	1.72	17.3	2.12
Moraceae								
(62)	55.4	2.71	39.0	6.38	14.7	3.54	21.2	3.85
(63)	48.0	4.70	37.4	3.71	12.1	3.05	21.3	3.19
(64)	71.6	0.42	53.2	3.08	27.3	1.87	25.8	1.38
(65)	47.5	2.47	38.3	2.60	22.8	1.15	17.9	1.02
(66)	60.7	-	34.2	-	26.6	-	20.8	-
Polygonaceae								
(67)	-	-	-	-	-	-	-	-
Rhamnaceae								
(68)	57.0	-	30.2	-	9.9	-	18.6	-
(69)	58.1	-	30.3	-	13.3	-	13.3	-
(70)	61.7	-	42.4	-	20.3	-	21.7	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A6. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Rubiaceae						
<i>Randia venezuelensis</i>	(71)	YL	Wet	2	18.0	3.79
<i>Randia venezuelensis</i>	(72)	NL	Wet	1	23.0	-
<i>Randia venezuelensis</i>	(73)	UF	Wet	1	19.9	-
Unidentified #01	(74)	L	Wet	3	29.9	6.84
Unidentified #01	(75)	YL	Wet	1	18.7	-
Rutaceae						
<i>Zanthoxylum culantrillo</i>	(76)	L	Wet	1	74.9	-
<i>Zanthoxylum culantrillo</i>	(77)	YL,L	Wet	2	33.4	0.55
<i>Zanthoxylum culantrillo</i>	(78)	YL	Wet	2	31.2	4.06
<i>Zanthoxylum culantrillo</i>	(79)	FLBU	Wet	2	31.7	-
Sapindaceae						
<i>Paullinia cururu</i>	(80)	L	Wet	4	41.3	2.00
Sterculiaceae						
<i>Guazuma ulmifolia</i>	(81)	F	Wet	2	18.6	-
<i>Guazuma ulmifolia</i>	(82)	UF	Dry	1	25.0	-
<i>Guazuma ulmifolia</i>	(83)	RF	Dry	2	58.3	40.60
<i>Guazuma ulmifolia</i>	(84)	FL	Dry	4	35.2	11.48

Table A6 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	CP (%)		EE (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rubiaceae								
(71)	20.8	0.01	2.8	0.46	4.5	0.10	4.87	0.10
(72)	ND	-	2.1	-	ND	-	4.75	-
(73)	14.2	-	1.3	-	4.6	-	4.54	-
(74)	16.6	1.56	4.1	2.57	7.5	0.90	4.61	0.07
(75)	ND	-	3.1	-	ND	-	4.99	-
Rutaceae								
(76)	12.5	-	1.3	-	5.9	-	4.78	-
(77)	12.6	0.07	2.7	0.21	5.1	0.12	4.95	0.25
(78)	14.1	0.76	1.9	1.01	4.1	0.13	4.81	0.11
(79)	15.8	0.42	2.1	0.12	5.8	0.81	5.01	0.20
Sapindaceae								
(80)	12.5	1.20	3.4	0.81	7.8	0.97	4.49	0.09
Sterculiaceae								
(81)	12.1	2.60	1.1	0.12	7.4	1.68	4.10	0.10
(82)	8.8	-	2.5	-	5.8	-	4.32	-
(83)	7.2	2.13	2.4	0.99	5.1	2.13	4.34	0.10
(84)	13.2	0.91	1.9	0.19	7.4	0.77	4.63	0.12

Table A6 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rubiaceae								
(71)	42.8	6.43	28.4	1.09	10.4	1.43	17.3	0.77
(72)	44.4	-	26.4	-	9.7	-	16.7	-
(73)	45.9	-	35.5	-	19.4	-	15.3	-
(74)	60.3	2.24	52.2	2.52	23.2	1.56	27.6	1.50
(75)	59.7	-	48.5	-	22.2	-	25.7	-
Rutaceae								
(76)	ND	-	55.5	-	40.0	-	15.7	-
(77)	48.0	2.95	41.5	7.37	25.5	3.64	16.3	1.31
(78)	44.5	3.33	34.6	2.15	14.2	2.80	19.6	4.80
(79)	48.0	5.24	36.9	5.47	21.4	5.12	15.2	0.61
Sapindaceae								
(80)	59.1	5.17	43.9	1.89	19.7	2.93	22.4	3.67
Sterculiaceae								
(81)	37.6	20.84	36.6	4.94	19.7	6.70	15.4	0.31
(82)	67.9	-	48.6	-	17.8	-	30.2	-
(83)	55.5	16.93	45.1	18.80	15.8	11.16	29.0	13.52
(84)	59.0	5.67	43.4	6.74	22.2	6.28	20.1	3.61

Table A7. Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Sterculiaceae (Cont'd)						
<i>Guazuma ulmifolia</i>	(85)	FL	Wet	1	19.0	-
<i>Sterculia apetala</i>	(86)	FL	Dry	1	ND	-
<i>Sterculia apetala</i>	(87)	FLBU	Dry	2	20.7	4.48
<i>Sterculia apetala</i>	(88)	FL(BU)	Dry	1	21.3	-
<i>Sterculia apetala</i>	(89)	ST	Dry	1	ND	-
UNIDENTIFIED PLANTS						
Unidentified #02	(90)	L	Dry	2	34.0	0.95
Unidentified #03	(91)	L	Dry	1	21.4	-

Table A7 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Crude Protein (%)		Ether Extract (%)		Ash (%)		GE (kcal/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Sterculiaceae								
(85)	20.1	-	2.4	-	8.1	-	4.57	-
(86)	ND	-	ND	-	ND	-	NE	-
(87)	9.3	0.21	2.2	0.31	6.9	0.52	4.25	0.04
(88)	11.7	-	1.6	-	7.2	-	4.43	-
(89)	ND	-	ND	-	ND	-	ND	-
UNIDENTIFIED								
(90)	18.1	0.71	0.8	0.13	6.5	0.15	4.55	0.06
(91)	15.1	-	3.1	-	4.7	-	4.98	-

Table A7 (cont'd). Proximate and fiber composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/sample	NDF (%)		ADF (%)		ADL (%)		Cellulose (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Sterculiaceae								
(85)	57.8	-	44	-	16.6	-	26.4	-
(86)	ND	-	ND	-	ND	-	ND	-
(87)	47.7	0.49	36.8	2.82	13.6	1.68	22.5	1.66
(88)	70.7	-	51.9	-	21.1	-	30.4	-
(89)	ND	-	ND	-	ND	-	ND	-
UNIDENTIFIED								
(90)	55.3	1.86	31.8	3.68	14.1	0.62	13.2	8.26
(91)	46.8	-	45.8	-	23.7	-	19.1	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A8. Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Anacardiaceae						
<i>Mangifera indica</i>	(1)	YL	Wet	1	20.6	-
<i>Mangifera indica</i>	(2)	UF	Dry	4	22.5	0.00
<i>Mangifera indica</i>	(3)	UF	Wet	1	19.0	-
<i>Mangifera indica</i>	(4)	RF	Dry	3	22.1	2.09
<i>Mangifera indica</i>	(5)	PUL	Dry	2	31.8	0.40
Annonaceae						
<i>Annona jahnii</i>	(6)	L	Wet	1	28.3	-
<i>Annona jahnii</i>	(7)	UF	Wet	1	30.2	-
<i>Annona jahnii</i>	(8)	RF	Wet	1	27.2	-
<i>Annona jahnii</i>	(9)	FL	Wet	1	19.1	-
<i>Annona punicifolia</i>	(10)	UF	Wet	1	16.0	-
<i>Annona punicifolia</i>	(11)	RF	Wet	3	36.8	25.90
Arecaceae						
<i>Copernicia tectorum</i>	(12)	F	Wet	2	28.2	2.90
<i>Copernicia tectorum</i>	(13)	UF	Dry	3	33.1	3.45
<i>Copernicia tectorum</i>	(14)	UF	Wet	1	ND	-
<i>Copernicia tectorum</i>	(15)	RF	Wet	1	27.8	-

Table A8 (cont'd). Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD			Mean	SD	Mean	SD	Mean	SD
Anacardiaceae												
(1)	0.20	-	0.33	-	0.61	-	39	-	2.10	-	0.27	-
(2)	0.12	0.03	0.06	0.00	2.00	2.40	52	2.40	1.49	0.06	0.15	0.03
(3)	0.06	-	0.02	-	3.00	-	29	-	1.21	-	0.09	-
(4)	0.11	0.01	0.06	0.02	1.83	9.48	48	9.48	1.46	0.47	0.04	0.01
(5)	3.47	0.27	0.21	0.00	16.52	31.79	184	31.79	2.75	0.37	0.42	0.06
Annonaceae												
(6)	2.04	-	0.18	-	11.33	-	76	-	1.67	-	0.24	-
(7)	0.05	-	0.14	-	0.36	-	30	-	1.72	-	0.29	-
(8)	0.11	-	0.22	-	0.50	-	53	-	1.56	-	0.25	-
(9)	0.46	-	0.29	-	1.59	-	52	-	2.01	-	0.29	-
(10)	0.21	-	0.15	-	1.40	-	87	-	1.30	-	0.20	-
(11)	0.16	0.03	0.21	0.03	0.76	10.68	53	10.68	1.38	0.25	0.17	0.02
Arecaeae												
(12)	0.29	0.04	0.12	0.04	2.42	51.09	122	51.09	2.28	1.36	0.38	0.21
(13)	0.24	0.02	0.12	0.01	2.00	30.26	146	30.26	3.11	0.47	0.23	0.13
(14)	0.26	-	0.11	-	2.36	-	118	-	3.06	-	0.26	-
(15)	0.22	-	0.09	-	2.44	-	117	-	2.39	-	0.20	-

Table A9. Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Asclepidaceae						
Marsdenia undulata	(16)	L	Wet	3	33.4	21.84
Marsdenia undulata	(17)	UF	Wet	1	10.0	-
Bombacaeae						
Ceiba pentandra	(18)	FLBU	Dry	1	20.2	-
Cactaceae						
Pereskia guamacho	(19)	RF	Wet	1	25.3	-
Chrysobalanaceae						
Licania pyrifolia	(20)	FL(BU)	Wet	1	30.6	-
Licania pyrifolia	(21)	NL	Dry	1	23.9	-
Licania pyrifolia	(22)	L	Dry	2	40.8	0.44
Cucurbitaceae						
Melothria trilobata	(23)	L	Wet	2	17.2	0.08
Dilleniaceae						
Tetracera volubris	(24)	FL	Wet	1	22.8	-
Euphorbiaceae						
Sapium aucuparium	(25)	L	Wet	3	67.0	2.41

Table A9 (cont'd). Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Asclepidaceae												
(16)	0.47	0.43	0.16	0.05	2.94	96	80.08	3.13	1.53	0.50	0.26	
(17)	0.11	-	0.08	-	1.38	68	-	1.66	-	0.18	-	
Bombacaceae												
(18)	1.05	-	0.33	-	3.18	82	-	3.05	-	0.39	-	
Cactaceae												
(19)	0.17	-	0.21	-	0.81	57	-	1.39	-	0.29	-	
Chrysobalanaceae												
(20)	0.17	-	0.18	-	0.94	93	-	1.37	-	0.19	-	
(21)	0.17	-	0.37	-	0.46	154	-	2.57	-	0.36	-	
(22)	0.31	0.05	0.15	0.00	2.07	118	9.62	1.38	0.06	0.28	0.01	
Cucurbitaceae												
(23)	2.95	0.79	0.29	0.06	10.17	96	8.28	2.63	1.40	0.45	0.14	
Dilleniaceae												
(24)	0.97	-	0.31	-	3.13	86	-	1.99	-	0.27	-	
Euphorbiaceae												
(25)	2.17	0.13	0.15	0.01	14.47	545	25.02	1.46	0.16	1.13	0.07	

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A10. Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part*	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Caesalpinoideae)						
<i>Cassia grandis</i>	(26)	L	Wet	3	51.6	12.13
<i>Cassia grandis</i>	(27)	UF	Wet	3	10.3	1.63
<i>Cassia moschata</i>	(28)	L	Wet	5	45.8	4.06
<i>Cassia moschata</i>	(29)	L	Dry	1	48.3	-
<i>Cassia moschata</i>	(30)	YL	Wet	1	32.9	-
<i>Cassia moschata</i>	(31)	YL	Dry	2	36.7	2.88
<i>Cassia moschata</i>	(32)	UF	Wet	3	20.3	1.49
Fabaceae (Mimosoideae)						
<i>Albizia columbiana</i>	(33)	L	Wet	1	81.0	-
<i>Albizia guachapele</i>	(34)	L	Wet	2	35.4	-
<i>Albizia guachapele</i>	(35)	L	Dry	1	37.1	-
<i>Albizia guachapele</i>	(36)	YL	Wet	1	28.7	-
<i>Albizia guachapele</i>	(37)	NL	Wet	3	31.0	1.98
<i>Enterolobium cyclocarpum</i>	(38)	F	Wet	-	-	-
<i>Pithecellobium dualense</i>	(39)	L	Wet	5	45.3	2.21
<i>Pithecellobium dualense</i>	(40)	FL/BU	Wet	2	22.2	0.74
<i>Pithecellobium saman</i>	(41)	L	Wet	7	38.3	7.44

Table A10 (cont'd). Macro mineral composition (dry basis) of plants consumed by red howlers (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family (Species no.)	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD			Mean	SD	Mean	SD	Mean	SD
Fabaceae												
(26)	1.91	0.28	0.11	0.30	17.36		50	6.20	0.54	0.17	0.40	0.50
(27)	0.26	0.02	0.29	0.01	0.90		53	4.93	2.62	1.36	0.28	0.03
(28)	1.34	0.62	0.11	0.02	12.18		47	25.31	0.51	0.21	0.51	0.09
(29)	2.21	-	0.13	-	17.00		48	-	0.56	-	0.38	-
(30)	0.31	-	0.14	-	2.21		33	-	1.17	-	0.15	-
(31)	0.18	0.04	0.24	0.03	0.75		80	25.37	1.30	0.07	0.48	0.61
(32)	0.16	0.02	0.16	0.02	1.00		38	15.08	1.65	0.47	0.14	0.01
Fabaceae												
(33)	1.01	-	0.14	-	7.21		160	-	0.74	-	0.21	-
(34)	0.65	0.34	0.19	0.05	3.42		99	33.19	1.40	0.03	0.39	0.01
(35)	0.31	-	0.22	-	1.41		114	-	1.18	-	0.25	-
(36)	0.27	-	0.30	-	0.90		25	-	1.81	-	0.25	-
(37)	0.16	0.03	0.42	0.05	0.38		45	3.32	1.69	0.07	0.26	0.01
(38)	ND		ND				ND		ND		ND	
(39)	0.99	0.09	0.11	0.03	9.00		42	11.38	0.61	0.04	0.61	1.12
(40)	0.36	0.06	0.44	0.01	0.82		47	20.85	2.30	0.13	0.21	0.04
(41)	0.60	0.31	0.14	0.04	4.29		161	65.35	0.83	0.28	0.24	0.31

* L= mature leaf; NL= new leaf; YL= young leaf; F= fruit; UF= unripe fruit; RF= ripe fruit; FL= flower; PF= petiole; PUL= pulvinus

Table A-11. Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part*	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Mimosoideae)						
<i>Pithecellobium saman</i>	(42)	L	Dry	2	36.9	1.06
<i>Pithecellobium saman</i>	(43)	NL	Dry	1	ND	ND
<i>Pithecellobium saman</i>	(44)	YL	Wet	3	24.5	1.29
<i>Pithecellobium saman</i>	(45)	FLBU	Dry	1	ND	ND
<i>Pithecellobium saman</i>	(46)	FL	Dry	2	19	1.00
<i>Pithecellobium saman</i>	(47)	RF	Dry	1	44	-
<i>Pithecellobium saman</i>	(48)	UF	Dry	2	22.5	-
<i>Pithecellobium tortum</i>	(49)	L	Wet	5	38	3.77
<i>Pithecellobium tortum</i>	(50)	YL	Wet	1	22.2	-
<i>Pithecellobium tortum</i>	(51)	FL	Wet	1	18.8	-
<i>Pithecellobium tortum</i>	(52)	BU,NL	Dry	2	41.8	0.11
<i>Pithecellobium tortum</i>	(53)	UF	Dry	1	71.4	-
Fabaceae (Papilionoideae)						
<i>Entada polystachya</i>	(54)	L	Wet	1	43.7	-
<i>Machaerium moritzianum</i>	(55)	FL	Dry	1	ND	-
<i>Platymiscium diadelphum</i>	(56)	L	Wet	1	37.5	-
<i>Platymiscium diadelphum</i>	(57)	YL,NL	Wet	1	31.2	-

Table A12. Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Papilionoideae) (cont'd)						
<i>Platymiscium polystachyum</i>	(58)	YL	Wet	1	21.2	-
<i>Platymiscium polystachyum</i>	(59)	FLBU	Wet	1	17.9	-
<i>Pterocarpus acapulcensis</i>	(60)	L	Wet	4	33.3	8.49
<i>Pterocarpus acapulcensis</i>	(61)	NL	Wet	4	27.6	1.77
Moraceae						
<i>Ficus pertusa</i>	(62)	L	Dry	3	26.5	16.32
<i>Ficus pertusa</i>	(63)	L	Wet	4	29.6	3.17
<i>Ficus pertusa</i>	(64)	UF	Wet	2	23.1	0.28
<i>Ficus pertusa</i>	(65)	RF	Wet	3	22.8	1.09
<i>Ficus trigonata</i>	(66)	UF	Wet	1	16.3	-
Polygonaceae						
<i>Coccoloba sp.</i>	(67)	YL	-	-	-	-
Rhamnaceae						
<i>Zizyphys saeri</i>	(68)	L	Wet	1	43.5	-
<i>Zizyphys saeri</i>	(69)	L	Dry	1	35.0	-
<i>Zizyphys saeri</i>	(70)	F	Wet	1	39.8	-

Table A12 (cont'd). Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD			Mean	SD	Mean	SD	Mean	SD
Fabaceae												
(58)	0.39	-	0.48	-	0.81	-	53	-	2.79	-	0.18	-
(59)	0.27	-	0.48	-	0.56	-	46	-	3.38	-	0.18	-
(60)	1.19	0.22	0.18	0.09	6.61	83	41.20	1.48	0.26	0.35	0.16	0.16
(61)	0.36	0.12	0.32	0.07	1.13	80	5.13	1.48	0.12	0.18	0.14	0.14
Moraceae												
(62)	4.45	3.69	0.13	0.04	34.23	310	33.46	0.93	0.35	0.80	0.11	0.11
(63)	2.89	0.16	0.11	0.02	26.27	226	141.1	1.67	0.42	0.50	0.21	0.21
(64)	1.14	0.16	0.16	0.01	7.12	146	30.39	1.96	0.26	1.52	2.12	2.12
(65)	0.74	0.03	0.12	0.02	6.17	108	19.61	1.52	0.24	0.31	0.01	0.01
(66)	0.74	-	0.23	-	3.22	377	-	1.95	-	0.27	-	-
Polygonaceae												
(67)	-	-	-	-	-	-	-	-	-	-	-	-
Rhamnaceae												
(68)	1.09	-	0.22	-	4.95	42	-	2.55	-	0.43	-	-
(69)	1.69	-	0.15	-	11.27	114	-	2.71	-	0.38	-	-
(70)	1.17	-	0.15	-	7.80	55	-	1.34	-	0.12	-	-

a L=leaves; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A13. Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Rubiaceae						
<i>Randia venezuelensis</i>	(71)	YL	Wet	2	18.0	3.79
<i>Randia venezuelensis</i>	(72)	NL	Wet	1	23.0	-
<i>Randia venezuelensis</i>	(73)	UF	Wet	1	19.9	-
Unidentified #01	(74)	L	Wet	3	29.9	6.84
Unidentified #01	(75)	YL	Wet	1	18.7	-
Rutaceae						
<i>Zanthoxylum culantrillo</i>	(76)	L	Wet	1	74.9	-
<i>Zanthoxylum culantrillo</i>	(77)	YL,L	Wet	2	33.4	0.55
<i>Zanthoxylum culantrillo</i>	(78)	YL	Wet	2	31.2	4.06
<i>Zanthoxylum culantrillo</i>	(79)	FLBU	Wet	2	31.7	-
Sapindaceae						
<i>Paullinia cururu</i>	(80)	L	Wet	4	41.3	2.00
Sterculiaceae						
<i>Guazuma ulmifolia</i>	(81)	F	Wet	2	18.6	-
<i>Guazuma ulmifolia</i>	(82)	UF	Dry	1	25.0	-
<i>Guazuma ulmifolia</i>	(83)	RF	Dry	2	58.3	40.60
<i>Guazuma ulmifolia</i>	(84)	FL	Dry	4	35.2	11.50

Table A13 (cont'd). Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD			Mean	SD	Mean	SD	Mean	SD
Rubiaceae												
(71)	0.80	0.35	0.38	0.05	2.11		58	3.1	1.82	0.58	0.27	0.03
(72)	0.53	-	0.27	-	1.96		49	-	2.43	-	0.32	-
(73)	0.36	-	0.19	-	1.89		58	-	2.12	-	0.18	-
(74)	1.16	0.19	0.14	0.02	8.29		101	39.3	2.24	0.18	0.41	0.04
(75)	0.84	-	0.31	-	2.71		92	-	3.15	-	0.33	-
Rutaceae												
(76)	0.82	-	0.12	-	6.83		46	-	0.98	-	0.72	-
(77)	0.68	0.01	0.16	0.02	4.25		93	11.8	0.90	0.02	0.88	0.17
(78)	0.40	0.01	0.16	0.04	2.50		195	161.9	1.47	0.44	0.39	0.01
(79)	0.66	-	0.24	-	2.75		119	-	1.85	-	0.47	-
Sapindaceae												
(80)	2.30	0.49	0.17	0.04	13.53		152	91.2	0.99	0.29	0.47	0.12
Sterculiaceae												
(81)	1.56	-	0.25	-	6.24		37	-	1.95	-	0.48	-
(82)	0.99	-	0.21	-	4.71		28	-	2.31	-	0.29	-
(83)	0.80	0.08	0.18	0.07	4.44		75	23.6	2.00	0.72	0.24	0.02
(84)	0.81	0.20	0.29	0.02	2.79		166	107.8	2.10	0.19	0.46	0.12

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PF=petiole;

Table A14. Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part*	Season	n	Dry matter (%)	
					Mean	SD
Sterculiaceae (Cont'd)						
Guazuma ulmifolia	(85)	FL	Wet	1	19.0	-
Sterculia apetala	(86)	FL	Dry	1	ND	-
Sterculia apetala	(87)	FLBU	Dry	2	20.7	4.48
Sterculia <u>apetala</u>	(88)	FL(BU)	Dry	1	21.3	-
Sterculia <u>apetala</u>	(89)	ST	Dry	1	ND	-
UNIDENTIFIED PLANTS						
Unidentified #02	(90)	L	Dry	2	34.0	0.95
Unidentified #03	(91)	L	Dry	1	21.4	-

Table A14 (cont'd). Macro mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Ca (%)		P (%)		Ca:P		Na (ppm)		K (%)		Mg (%)	
	Mean	SD	Mean	SD			Mean	SD	Mean	SD	Mean	SD
Sterculiaceae												
(85)	0.87	-	0.46	-	1.89		149	-	3.33	-	2.53	-
(86)	ND	-	ND	-	ND		ND	-	ND	-	ND	-
(87)	0.56	0.19	0.31	0.02	1.81		105	20.83	2.59	0.53	0.47	0.11
(88)	0.55	-	0.26	-	2.12		41	-	2.32	-	0.40	-
(89)	ND	-	ND	-			ND	-		-	ND	-
UNIDENTIFIED												
(90)	1.45	0.32	0.16	0.01	9.06		99	8.47	2.57	0.69	0.59	0.15
(91)	0.40	-	0.29	-	1.38		68	-	2.53	-	0.39	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A15. Trace mineral composition (dry basis) of plants consumed by red howler monkeys (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Anacardiaceae						
<i>Mangifera indica</i>	(1)	YL	Wet	1	20.6	-
<i>Mangifera indica</i>	(2)	UF	Dry	4	22.5	0.00
<i>Mangifera indica</i>	(3)	UF	Wet	1	19.0	-
<i>Mangifera indica</i>	(4)	RF	Dry	3	22.1	2.09
<i>Mangifera indica</i>	(5)	PUL	Dry	2	31.8	0.40
Annonaceae						
<i>Annona jahnii</i>	(6)	L	Wet	1	28.3	-
<i>Annona jahnii</i>	(7)	UF	Wet	1	30.2	-
<i>Annona jahnii</i>	(8)	RF	Wet	1	27.2	-
<i>Annona jahnii</i>	(9)	FL	Wet	1	19.1	-
<i>Annona puniceifolia</i>	(10)	UF	Wet	1	16.0	-
<i>Annona puniceifolia</i>	(11)	RF	Wet	3	36.8	25.90
Areaceae						
<i>Copernicia tectorum</i>	(12)	F	Wet	2	28.2	2.90
<i>Copernicia tectorum</i>	(13)	UF	Dry	3	33.1	3.45
<i>Copernicia tectorum</i>	(14)	UF	Wet	1	ND	-
<i>Copernicia tectorum</i>	(15)	RF	Wet	1	27.8	-

Table A15. Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Anacardiaceae										
(1)	35.19	-	13.26	-	113.40	-	0.11	-	30.82	-
(2)	10.57	1.26	4.60	0.55	21.28	1.40	0.03	0.01	5.45	0.40
(3)	28.70	-	6.10	-	14.78	-	0.04	-	6.89	-
(4)	16.56	3.00	4.99	0.82	28.53	8.51	0.02	0.01	9.56	4.26
(5)	28.37	2.08	4.54	0.65	348.56	6.94	0.08	0.00	57.94	5.46
Annonaceae										
(6)	154.90	-	16.59	-	690.03	-	0.10	-	21.99	-
(7)	31.88	-	13.28	-	193.40	-	0.01	-	19.40	-
(8)	37.02	-	19.11	-	29.64	-	0.03	-	16.34	-
(9)	76.82	-	29.70	-	223.99	-	0.01	-	35.65	-
(10)	21.34	-	17.07	-	13.60	-	0.06	-	17.84	-
(11)	28.23	4.14	14.73	3.15	10.74	1.07	0.05	0.02	14.14	1.19
Arecaceae										
(12)	34.66	13.80	8.81	2.54	67.01	35.65	1.33	0.77	25.70	15.16
(13)	29.25	6.00	10.95	1.39	51.34	11.36	0.68	0.34	15.75	0.94
(14)	235.49	-	11.08	-	32.71	-	0.20	-	17.88	-
(15)	50.44	-	7.64	-	18.84	-	0.18	-	16.62	-

Table A16. Trace mineral composition (dry basis) of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Asclepidaceae						
Marsdenia undulata	(16)	L	Wet	3	33.4	21.84
Marsdenia undulata	(17)	UF	Wet	1	10.0	-
Bombacaeae						
Ceiba pentandra	(18)	FLBU	Dry	1	20.2	-
Cactaceae						
Pereskia guamacho	(19)	RF	Wet	1	25.3	-
Chrysobalanaceae						
Licania pyrifolia	(20)	FL(BU)	Wet	1	30.6	-
Licania pyrifolia	(21)	NL	Dry	1	23.9	-
Licania pyrifolia	(22)	L	Dry	2	40.8	0.44
Cucurbitaceae						
Melothria trilobata	(23)	L	Wet	2	17.2	0.08
Dilleniaceae						
Tetracera volubris	(24)	FL	Wet	1	22.8	-
Euphorbiaceae						
Sapium aucuparium	(25)	L	Wet	3	67.0	2.41

Table A16 (cont'd). Trace mineral composition (dry basis) of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Asclepidaceae										
(16)	199.64	66.62	16.63	3.49	944.92	443.52	0.04	0.02	27.77	1.82
(17)	25.65	-	8.13	-	66.97	-	0.04	-	14.64	-
Bombaceae										
(18)	30.92	-	15.79	-	22.33	-	0.05	-	17.41	-
Cactaceae										
(19)	26.51	-	9.19	-	42.38	-	0.03	-	30.09	-
Chrysobalanaceae										
(20)	49.97	-	17.68	-	125.49	-	0.04	-	18.62	-
(21)	133.92	-	16.03	-	66.91	-	0.21	-	25.88	-
(22)	52.37	6.58	11.02	0.63	200.27	8.99	0.15	0.04	16.84	0.88
Cucurbitaceae										
(23)	142.80	40.11	13.64	0.81	104.64	70.20	0.05	0.01	34.25	4.75
Dilleniaceae										
(24)	42.29	-	13.91	-	83.52	-	0.08	-	21.55	-
Euphorbiaceae										
(25)	93.23	16.40	10.07	1.76	86.08	4.26	0.06	0.00	100.90	6.41

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A17. Trace mineral composition (dry basis) of plants consumed by red howler monkeys (*Alouatta seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Caesalpinoideae)						
<i>Cassia grandis</i>	(26)	L	Wet	3	51.6	12.13
<i>Cassia grandis</i>	(27)	UF	Wet	3	10.3	1.63
<i>Cassia moschata</i>	(28)	L	Wet	5	45.8	4.06
<i>Cassia moschata</i>	(29)	L	Dry	1	48.3	-
<i>Cassia moschata</i>	(30)	YL	Wet	1	32.9	-
<i>Cassia moschata</i>	(31)	YL	Dry	2	36.7	2.88
<i>Cassia moschata</i>	(32)	UF	Wet	3	20.3	1.49
Fabaceae (Mimosoideae)						
<i>Albizia columbiana</i>	(33)	L	Wet	1	81.0	-
<i>Albizia guachapele</i>	(34)	L	Wet	2	35.4	-
<i>Albizia guachapele</i>	(35)	L	Dry	1	37.1	-
<i>Albizia guachapele</i>	(36)	YL	Wet	1	28.7	-
<i>Albizia guachapele</i>	(37)	NL	Wet	3	31.0	1.98
<i>Enterolobium cyclocarpum</i>	(38)	F	Wet	-	-	-
<i>Pithecellobium dualense</i>	(39)	L	Wet	5	45.3	2.21
<i>Pithecellobium dualense</i>	(40)	FL/BU	Wet	2	22.2	0.74
<i>Pithecellobium saman</i>	(41)	L	Wet	7	38.3	7.44

Table A17 (cont'd). Trace mineral composition (dry basis) of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae										
(26)	220.03	158.28	4.77	0.85	66.52	47.53	0.23	0.15	12.95	3.06
(27)	34.03	4.00	10.23	0.46	21.41	1.86	0.21	0.27	18.03	0.87
(28)	251.62	95.87	5.63	0.28	331.70	109.88	0.11	0.01	23.21	6.99
(29)	178.50	-	5.32	-	224.64	-	0.05	-	5.32	-
(30)	29.55	-	8.27	-	123.24	-	0.08	-	14.25	-
(31)	174.72	4.89	9.96	1.95	50.19	25.98	0.08	0.03	15.64	3.68
(32)	28.48	2.76	7.01	0.43	51.01	6.53	0.04	0.02	11.00	2.82
Fabaceae										
(33)	197.41	-	10.00	-	458.82	-	0.15	-	15.29	-
(34)	80.56	21.89	7.79	3.26	42.19	10.94	0.10	0.00	23.18	10.61
(35)	146.78	-	8.02	-	41.14	-	0.41	-	18.19	-
(36)	76.24	-	6.94	-	27.72	-	0.87	-	32.03	-
(37)	92.59	18.94	15.02	1.81	25.72	15.23	0.40	0.29	50.60	9.51
(38)	-	-	-	-	-	-	-	-	-	-
(39)	147.57	37.41	13.52	2.93	505.70	45.15	0.31	0.13	12.48	1.72
(40)	48.53	0.97	27.80	0.58	59.56	2.21	0.32	0.01	53.86	0.83
(41)	118.02	22.87	9.59	2.47	33.19	7.27	0.19	0.06	9.03	3.48

* L=late leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

Table A18. Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part*	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Mimosoideae)						
<i>Pithecellobium saman</i>	(42)	L	Dry	2	36.9	1.06
<i>Pithecellobium saman</i>	(43)	NL	Dry	1	ND	ND
<i>Pithecellobium saman</i>	(44)	YL	Wet	3	24.5	1.29
<i>Pithecellobium saman</i>	(45)	FLBU	Dry	1	ND	ND
<i>Pithecellobium saman</i>	(46)	FL	Dry	2	19.0	1.00
<i>Pithecellobium saman</i>	(47)	RF	Dry	1	44.0	-
<i>Pithecellobium saman</i>	(48)	UF	Dry	2	22.5	-
<i>Pithecellobium tortum</i>	(49)	L	Wet	5	38.0	3.77
<i>Pithecellobium tortum</i>	(50)	YL	Wet	1	22.2	-
<i>Pithecellobium tortum</i>	(51)	FL	Wet	1	18.8	-
<i>Pithecellobium tortum</i>	(52)	BU,NL	Dry	2	41.8	0.11
<i>Pithecellobium tortum</i>	(53)	UF	Dry	1	71.4	-
Fabaceae (Papilionoideae)						
<i>Entada polystachya</i>	(54)	L	Wet	1	43.7	-
<i>Machaerium moritzianum</i>	(55)	FL	Dry	1	ND	-
<i>Platymiscium diadelphum</i>	(56)	L	Wet	1	37.5	-
<i>Platymiscium diadelphum</i>	(57)	YL,NL	Wet	1	31.2	-

Table A18 (cont'd). Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae										
(42)	74.71	4.65	10.59	0.67	17.48	0.29	0.23	0.09	11.26	0.34
(43)	162.04	-	22.54	-	17.49	-	0.25	-	45.81	-
(44)	67.44	9.10	14.20	2.63	18.23	1.33	0.37	0.12	21.86	5.89
(45)	88.31	-	21.45	-	26.71	-	0.37	-	47.64	-
(46)	163.05	105.71	13.53	1.19	19.62	1.02	0.43	0.33	23.19	1.05
(47)	19.54	-	6.58	-	11.45	-	0.12	-	7.04	-
(48)	26.98	3.13	7.67	0.65	10.21	4.68	0.14	0.02	14.20	0.54
(49)	241.98	248.43	8.12	1.04	179.79	45.94	0.09	0.03	8.01	1.41
(50)	85.53	-	24.21	-	108.27	-	0.06	-	27.77	-
(51)	47.87	-	23.36	-	59.23	-	0.09	-	29.22	-
(52)	51.69	8.39	21.47	7.81	56.28	20.67	0.23	0.17	28.75	10.42
(53)	1.27	-	12.58	-	40.39	-	0.79	-	10.44	-
Fabaceae										
(54)	102.20	-	11.44	-	69.98	-	0.03	-	13.63	-
(55)	59.62	-	20.72	-	22.06	-	0.52	-	32.03	-
(56)	128.87	-	20.94	-	111.66	-	0.07	-	31.38	-
(57)	57.03	-	23.40	-	53.67	-	0.10	-	49.75	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PF=petiole; PUL=pulvinus

Table A19. Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Fabaceae (Papilionoideae) (cont'd)						
<i>Platymiscium polystachyum</i>	(58)	YL	Wet	1	21.2	-
<i>Platymiscium polystachyum</i>	(59)	FLBU	Wet	1	17.9	-
<i>Pterocarpus acapulcensis</i>	(60)	L	Wet	4	33.3	8.49
<i>Pterocarpus acapulcensis</i>	(61)	NL	Wet	4	27.6	1.77
Moraceae						
<i>Ficus pertusa</i>	(62)	L	Dry	3	26.5	16.32
<i>Ficus pertusa</i>	(63)	L	Wet	4	29.6	3.17
<i>Ficus pertusa</i>	(64)	UF	Wet	2	23.1	0.28
<i>Ficus pertusa</i>	(65)	RF	Wet	3	22.8	1.09
<i>Ficus trigonata</i>	(66)	UF	Wet	1	16.3	-
Polygonaceae						
<i>Coccoloba sp.</i>	(67)	YL	-	-	-	-
Rhamnaceae						
<i>Zizyphys saeri</i>	(68)	L	Wet	1	43.5	-
<i>Zizyphys saeri</i>	(69)	L	Dry	1	35.0	-
<i>Zizyphys saeri</i>	(70)	F	Wet	1	29.8	-

Table A19 (cont'd). Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Fabaceae										
(58)	60.14	-	28.84	-	34.70	-	0.24	-	57.23	-
(59)	65.11	-	35.49	-	30.58	-	0.37	-	58.52	-
(60)	320.78	159.92	16.37	5.62	273.45	55.72	0.27	0.02	24.78	9.29
(61)	97.33	14.49	20.05	2.14	145.92	122.50	0.08	0.01	37.12	2.35
Moraceae										
(62)	162.08	14.32	5.89	0.98	34.27	16.61	0.31	0.06	13.62	2.37
(63)	238.13	102.87	7.20	1.00	105.37	19.42	0.04	0.01	16.54	1.13
(64)	81.30	5.76	13.09	1.22	43.69	1.57	0.05	0.02	21.14	1.26
(65)	56.62	4.33	9.15	1.59	30.14	0.68	0.03	0.01	14.17	1.96
(66)	49.93	-	12.98	-	42.48	-	0.10	-	26.88	-
Polygonaceae										
(67)	-	-	-	-	-	-	-	-	-	-
Rhamnaceae										
(68)	90.09	-	20.22	-	119.85	-	17.59	-	40.70	-
(69)	215.32	-	9.91	-	66.19	-	1.02	-	20.70	-
(70)	51.54	-	8.86	-	154.10	-	77.40	-	10.43	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; BR=branch

Table A20. Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Rubiaceae						
<i>Randia venezuelensis</i>	(71)	YL	Wet	2	18.0	3.79
<i>Randia venezuelensis</i>	(72)	NL	Wet	1	23.0	-
<i>Randia venezuelensis</i>	(73)	UF	Wet	1	19.9	-
Unidentified #01	(74)	L	Wet	3	29.9	6.84
Unidentified #01	(75)	YL	Wet	1	18.7	-
Rutaceae						
<i>Zanthoxylum culantrillo</i>	(76)	L	Wet	1	74.9	-
<i>Zanthoxylum culantrillo</i>	(77)	YL,L	Wet	2	33.4	0.55
<i>Zanthoxylum culantrillo</i>	(78)	YL	Wet	2	31.2	4.06
<i>Zanthoxylum culantrillo</i>	(79)	FLBU	Wet	2	31.7	-
Sapindaceae						
<i>Paullinia cururu</i>	(80)	L	Wet	4	41.3	2.00
Sterculiaceae						
<i>Guazuma ulmifolia</i>	(81)	F	Wet	2	18.6	-
<i>Guazuma ulmifolia</i>	(82)	UF	Dry	1	25.0	-
<i>Guazuma ulmifolia</i>	(83)	RF	Dry	2	58.3	40.60
<i>Guazuma ulmifolia</i>	(84)	FL	Dry	4	35.2	11.50

Table A20 (cont'd). Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rubiaceae										
(71)	100.67	10.59	19.50	5.53	85.26	12.93	0.14	0.00	24.94	6.04
(72)	91.60	-	13.33	-	79.99	-	0.20	-	19.15	-
(73)	37.68	-	7.94	-	42.27	-	0.05	-	8.48	-
(74)	172.23	69.88	18.04	1.33	52.78	7.68	0.09	0.05	26.20	2.21
(75)	94.92	-	26.08	-	61.19	-	0.20	-	30.99	-
Rutaceae										
(76)	323.75	-	13.49	-	721.64	-	0.06	-	17.83	-
(77)	141.16	4.65	13.07	2.96	372.52	7.20	0.18	0.21	41.69	30.90
(78)	126.01	4.45	10.99	5.24	274.87	7.79	0.07	0.02	13.50	4.74
(79)	64.01	-	20.97	-	390.85	-	0.04	-	27.22	-
Sapindaceae										
(80)	358.11	134.34	14.15	0.67	112.57	34.78	0.16	0.14	16.48	1.89
Sterculiaceae										
(81)	40.03	-	16.05	-	59.89	-	0.03	-	23.90	-
(82)	42.07	-	12.50	-	31.17	-	0.03	-	18.41	-
(83)	46.04	5.15	21.40	3.20	42.35	4.69	0.04	0.02	15.88	2.05
(84)	341.55	78.99	17.86	1.66	74.21	6.17	0.15	0.18	24.85	2.34

Table A21. Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Species	Species no.	Part ^a	Season	n	Dry matter (%)	
					Mean	SD
Sterculiaceae (Cont'd)						
<i>Guazuma ulmifolia</i>	(85)	FL	Wet	1	19.0	-
<i>Sterculia apetala</i>	(86)	FL	Dry	1	ND	-
<i>Sterculia apetala</i>	(87)	FLBU	Dry	2	20.7	4.48
<i>Sterculia apetala</i>	(88)	FL(BU)	Dry	1	21.3	-
<i>Sterculia apetala</i>	(89)	ST	Dry	1	ND	-
UNIDENTIFIED PLANTS						
Unidentified #02	(90)	L	Dry	2	34.0	0.95
Unidentified #03	(91)	L	Dry	1	21.4	-

Table A21 (cont'd). Trace mineral composition of plants consumed by red howler monkeys (*Alouatta seniculus seniculus*) in the central llanos region of Venezuela.

Family/ Sample	Fe (ppm)		Cu (ppm)		Mn (ppm)		Se (ppm)		Zn (ppm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Sterculiaceae										
(85)	145.24	-	18.02	-	36.45	-	0.05	-	31.00	-
(86)	ND	-	ND	-	ND	-	ND	-	ND	-
(87)	82.42	4.64	13.04	0.92	70.50	30.56	0.08	0.01	41.74	4.51
(88)	73.07	-	16.18	-	17.37	-	0.07	-	48.52	-
(89)	ND	-	ND	-	ND	-	ND	-	ND	-
UNIDENTIFIED										
(90)	159.24	7.30	13.20	0.77	42.99	6.96	0.34	0.01	44.31	8.84
(91)	97.55	-	19.89	-	42.81	-	0.49	-	39.77	-

* L=mature leaf; NL=new leaf; YL=young leaf; F=fruit; UF=unripe fruit; RF=ripe fruit; FL=flower; PET=petiole; PUL=pulvinus

APPENDIX B

Table B1. Body weights (BW) of study subjects prior to, during, and following feeding trials.

Species	ID	Sex	Body weight (kg)		
			Pre-study	Crossover	Post-study
<i>Varecia variegata rubra</i>	Athena	♀	4.50	4.05	4.05
	Michele	♀	4.30	3.70	3.60
	Rinda	♀	5.30	4.30	-
	Spica	♀	4.95	4.25	4.25
<i>Varecia variegata variegata</i>	Ino	♀	4.65	4.40	4.45
	Night	♀	5.00	3.80	3.80
<i>Alouatta caraya</i>	Phoebe	♀	4.72	-	-
	Katie	♀	8.94	-	-
	Jessie	♀	7.44	-	-
	Shadow	♂	10.66	-	-
<i>Alouatta seniculus sara</i>	Pilgrim	♂	9.15	8.55	-
	Howie	♂	7.50	7.90	7.60
<i>Alouatta villosa palliata</i>	Jalapeno	♂	5.15	6.05	6.75
	Waldo	♂	6.85	6.55	5.80

Table B1 (cont'd). Body weights (BW) of study subjects prior to, during, and following feeding trials.

Species	ID	Sex	Body weight (kg)		
			Pre-study	Crossover	Post-study
<i>Colobus guereza kikuyuensis</i>	Flower	♀	11.34	-	-
	Gomez	♂	10.70	10.90	10.65
<i>Trachypithecus f. francoisi</i>	Jack	♂	7.78	-	7.71
	Janet	♀	5.67	-	5.72
	Chrissie	♀	6.67	-	5.76
	Stanley	♂	3.76	-	3.99
	Fungar	♂	5.75	6.75	7.25
	GooNgoot	♂	5.85	6.05	-
<i>Pygathrix nemaeus nemaeus</i>	Rhett	♂	11.75	12.10	12.40
<i>Cercopithecus g. chrysogaster</i>	Heine	♂	9.60	10.10	10.30
<i>Mandrillus l. leucophaeus</i>	Susie	♀	10.20	10.00	8.90

Table B2. Body weight (BW) and dry matter intake (DMI) of ruffed lemurs (*Varecia spp.*) fed diet 15ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a						
				DM	NDF	ADF	C	HC	ADL	
<i>Varecia variegata rubra</i>	Athena	4.50	32.5	51.9	22.2	8.9	13.3	43.7	23.2	
	Michele	4.30	21.5	56.7	24.2	17.6	15.2	34.8	33.8	
	Rinda	5.30	17.8	56.2	26.9	20.4	17.0	37.3	22.8	
	Spica	4.95	36.0	51.2	22.4	9.9	17.3	42.4	48.1	
	Mean	4.76	26.9	54.0	23.9	14.2	15.7	39.5	32.0	
	SD	0.45	8.7	2.9	2.2	5.7	1.9	4.2	11.9	
<i>Varecia variegata variegata</i>	Ino	4.65	29.8	43.7	15.6	5.2	8.7	35.6	27.2	
	Night	5.00	25.2	51.6	17.7	5.5	3.1	37.3	83.1	
	Mean	4.83	27.5	47.7	16.6	5.3	5.9	36.5	55.1	
	SD	0.25	3.3	5.6	1.5	0.2	4.0	1.2	39.5	
<i>Varecia variegata ssp.</i>	Mean	4.78	27.1	51.9	21.5	11.3	12.4	38.5	39.7	
	SD	0.37	6.9	4.7	4.2	6.3	5.5	3.7	23.3	

^aDM=dry matter; NDF=neutral-detergent fiber; ADF=acid-detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid-detergent lignin

Table B3. Body weight (BW) and dry matter intake (DMI) of ruffed lemurs (*Varecia* spp.) fed diet 30ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a					
				DM	NDF	ADF	C	HC	ADL
<i>Varecia variegata rubra</i>	Athena	4.05	45.2	43.5	23.3	14.7	12.6	42.6	62.3
	Michele	3.70	38.7	45.2	23.3	15.2	9.7	41.4	59.2
	Spica	4.25	53.0	34.8	10.5	1.8	-2.6	30.0	62.8
	Mean	4.00	45.6	41.2	19.0	10.6	6.6	38.0	61.4
	SD	0.28	7.2	5.6	7.4	7.6	8.1	7.0	2.0
<i>Varecia variegata variegata</i>	Ino	4.40	63.8	48.8	29.3	24.1	20.0	40.8	28.0
	Night	3.80	73.9	36.2	17.3	7.4	3.8	39.8	37.1
	Mean	4.10	68.8	42.5	23.3	15.8	11.9	40.3	32.5
	SD	0.42	7.1	8.9	8.5	11.8	11.5	0.7	6.4
<i>Varecia variegata ssp.</i>	Mean	4.04	54.9	41.7	20.7	12.6	8.7	38.9	49.9
	SD	0.30	14.2	6.0	7.1	8.5	8.6	5.1	16.2

^aDM=dry matter; NDF=neutral-detergent fiber; ADF=acid-detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid-detergent lignin

Table B4. Body weight (BW) of ruffed lemurs (*Varecia spp.*) fed diets 15ADF and 30ADF and the apparent digestibility of dry matter and gross energy in those diets.^a

Species	ID	15ADF				30ADF		
		BW (kg)	DM (%)	GE (%)	DE (kcal/g)	DM (%)	GE (%)	DE (kcal/g)
<i>Varecia variegata rubra</i>	Athena	4.50	51.9	43.0	1.92	43.5	41.6	1.82
	Michele	4.30	56.7	54.5	2.43	45.2	44.9	1.97
	Rinda	5.30	56.2	52.1	2.37	-	-	-
	Spica	4.95	51.2	48.9	2.18	34.8	30.7	1.35
	Mean	4.76	54.0	49.6	2.23	41.2	39.1	1.71
<i>Varecia variegata variegata</i>	SD	0.45	2.85	4.98	0.23	5.58	7.43	0.32
	Ino	4.65	43.7	43.0	1.92	48.8	46.9	2.06
	Night	5.00	51.6	45.7	2.57	36.2	34.6	1.52
	Mean	4.83	47.7	44.4	2.25	42.5	40.8	1.79
	SD	0.25	5.59	1.91	0.46	8.91	8.70	0.38
<i>Varecia variegata ssp.</i>	Mean	4.78	51.9	47.9	2.23	41.7	39.7	1.74
	SD	0.37	4.68	4.80	0.27	5.99	6.88	0.30

^aDM=dry matter; GE=gross energy; DE=digestible energy

Table B5. Body weight (BW) and dry matter intake (DMI) of howler monkeys (*Alouatta* spp.) fed diet 15ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a					
				DM	NDF	ADF	C	HC	ADL
<i>Alouatta caraya</i>	Phoebe	4.72	24.9	64.5	38.2	29.6	28.1	44.3	28.7
	Katie	8.94	17.3	67.9	44.4	37.9	36.4	54.8	57.4
	Jessie	7.44	15.6	70.2	43.5	40.2	37.4	49.0	67.2
	Shadow	10.66	10.5	70.7	57.0	54.1	49.5	61.8	68.0
	Mean	7.94	17.1	68.3	45.8	40.5	37.9	52.5	55.3
	SD	2.52	17.10	2.8	8.0	10.2	8.8	7.6	18.4
<i>Alouatta villosa palliata</i>	Jalapeno	5.15	21.7	69.4	47.3	45.9	42.5	49.4	58.2
	Waldo	6.55	26.0	70.6	40.1	41.7	36.6	54.3	76.7
	Mean	5.85	23.8	70.0	43.7	43.8	39.5	51.8	67.5
	SD	0.99	3.05	0.9	5.1	3.0	4.2	3.5	13.1
<i>Alouatta seniculus sara</i>	Pilgrim	9.15	11.8	76.7	53.6	56.7	57.4	48.6	71.1
	Howie	7.50	20.4	65.2	33.2	29.5	24.1	39.0	59.1
	Mean	8.32	16.1	71.0	43.4	43.1	40.8	43.8	65.1
	SD	1.17	6.12	8.1	14.4	19.2	21.2	6.8	8.5
<i>Alouatta spp.</i>	Mean	7.51	18.5	69.4	44.7	42.0	39.0	50.1	60.8
	SD	2.03	5.73	3.8	7.9	10.1	10.8	6.9	14.7

Table B6. Body weight (BW) and dry matter intake (DMI) of howler monkeys (*Alouatta* spp.) fed diet 30ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a					
				DM	NDF	ADF	C	HC	ADL
<i>Alouatta caraya</i>	Phoebe	4.72	38.4	61.0	41.2	34.2	33.0	56.8	38.3
	Katie	8.94	18.7	63.7	50.6	43.3	42.9	66.7	57.3
	Shadow	10.66	19.4	61.4	45.5	35.7	34.5	67.3	56.2
	Mean	8.11	25.5	62.0	45.8	37.7	36.8	63.6	50.6
	SD	3.06	11.18	1.5	4.7	4.9	5.3	5.9	10.7
<i>Alouatta villosa palliata</i>	Jalapeno	6.05	18.4	62.6	55.9	50.2	50.4	68.6	64.3
	Waldo	6.85	22.2	61.6	49.2	42.1	38.5	64.9	60.3
	Mean	6.45	20.3	62.1	52.5	46.2	44.5	66.8	62.3
	SD	0.57	2.67	0.7	4.7	5.7	8.4	2.6	2.8
<i>Alouatta seniculus sara</i>	Pilgrim	8.55	19.0	61.0	47.0	43.6	42.4	54.5	56.2
	Howie	7.50	20.4	60.3	42.5	35.3	32.1	58.3	59.7
	Mean	8.03	19.7	60.6	44.8	39.5	37.3	56.4	58.0
	SD	0.74	0.95	0.5	3.2	5.9	7.3	2.7	2.5
<i>Alouatta</i> spp.	Mean	7.61	22.4	61.7	47.4	40.6	39.1	62.4	56.0
	SD	1.97	7.2	1.1	5.0	5.8	6.6	5.7	8.3

^aDM=dry matter; NDF=neutral detergent fiber; ADF=acid detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid

Table B7. Body weight (BW) howler monkeys (*Alouatta* spp.) fed diets 15ADF and 30ADF and the apparent digestibility of dry matter and gross energy in those diets.^a

Species	ID	15ADF				30ADF		
		BW (kg)	DM (%)	GE (%)	DE (kcal/g)	DM (%)	GE (%)	DE (kcal/g)
<i>Alouatta caraya</i>	Phoebe	4.72	64.5	62.6	2.79	61.0	60.7	2.66
	Katie	8.94	67.9	68.0	3.03	63.7	64.5	2.83
	Jessie	7.44	70.2	71.6	3.19	-	-	-
	Shadow	10.66	70.7	68.6	3.06	61.4	59.7	2.62
	Mean	7.94	68.3	67.7	3.02	62.0	61.6	2.70
<i>Alouatta villosa palliata</i>	SD	2.52	2.83	3.75	0.17	1.46	2.53	0.11
	Jalapeno	5.15	69.4	68.6	3.06	62.6	61.7	2.71
	Waldo	6.55	70.6	69.0	3.08	61.6	61.8	2.71
	Mean	5.85	70.0	68.8	3.07	62.1	61.8	2.71
	SD	0.99	0.85	0.28	0.01	0.71	0.07	0.00
<i>Alouatta seniculus sara</i>	Pilgrim	9.15	76.7	77.3	3.45	63.4	61.7	2.71
	Howie	7.50	65.2	65.7	2.93	60.3	60.5	2.65
	Mean	8.32	71.0	71.5	3.19	61.8	61.1	2.68
	SD	1.17	8.13	8.20	0.37	2.19	0.85	0.04
<i>Alouatta</i> spp.	Mean	7.51	69.4	68.9	3.07	62.0	61.5	2.70
	SD	2.03	3.80	4.29	0.19	1.27	1.53	0.07

Table B8. Body weight (BW) and dry matter intake (DMI) of colobines fed diet 15ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a					
				DM	NDF	ADF	C	HC	ADL
<i>Colobus g. kikuyuensis</i>	Flower	11.34	16.3	73.5	39.7	30.2	40.2	54.9	-16.3
	Gomez	10.90	14.2	80.3	77.0	80.1	81.4	67.9	84.5
	Mean	11.12	15.3	76.9	58.4	55.1	60.8	61.4	34.1
	SD	0.31	1.48	4.8	26.4	35.3	29.1	9.2	71.3
	Rhett	12.10	35.5	76.2	66.5	66.6	59.7	66.4	78.4
<i>Pygathrix n. nemaeus</i>									
<i>Trachypithecus f. francoisi</i>	Jack	7.71	23.7	84.6	80.5	81.4	82.2	79.1	83.7
	Janet	5.67	24.8	79.7	77.7	81.4	90.4	71.8	51.8
	Chrissie	6.67	32.7	82.9	83.4	88.2	88.3	71.9	83.6
	Stanley	3.99	42.3	85.9	83.9	85.0	87.6	82.2	87.8
	Fungar	5.75	34.7	78.9	70.9	75.4	73.1	63.7	71.8
	Mean	5.96	31.6	82.4	79.3	82.3	84.3	73.7	75.7
	SD	1.38	7.65	3.0	5.3	4.8	7.0	7.2	14.7
Colobines	Mean	8.02	28.0	80.3	72.5	73.5	75.4	69.7	65.7
	SD	3.04	9.88	4.1	14.5	18.7	17.4	8.6	35.1

^aDM=dry matter; NDF=neutral-detergent fiber; ADF=acid-detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid-detergent lignin

Table B9. Body weight (BW) and dry matter intake (DMI) of colobines fed diet 30ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a					
				DM	NDF	ADF	C	HC	ADL
<i>Colobus g. kikuyuensis</i>	Gomez	10.70	14.4	78.7	74.3	56.2	76.1	78.0	77.2
	Rhett	11.75	33.3	73.9	69.8	67.6	66.1	74.8	82.5
<i>Trachypithecus f. francoisi</i>	Jack	7.78	23.1	79.9	82.6	84.5	87.6	78.2	61.9
	Janet	5.72	18.1	74.4	81.5	83.2	89.8	77.7	49.4
	Chrissie	5.76	38.2	77.0	74.8	72.3	72.7	80.4	78.4
	Stanley	3.77	37.8	80.1	76.6	76.0	76.5	77.9	71.4
	Fungar	6.75	35.2	72.0	63.2	59.2	57.9	72.2	70.1
	Goongoot	5.85	38.1	81.1	76.3	72.2	73.7	85.3	60.1
Colobines	Mean	5.94	31.8	77.4	75.8	74.6	76.4	78.6	65.2
	SD	1.33	8.8	3.6	6.9	9.2	11.6	4.3	10.2
Colobines	Mean	7.26	29.8	77.1	74.9	71.4	75.1	78.1	68.9
	SD	2.71	9.7	3.4	6.2	10.2	10.4	3.8	11.1

^aDM=dry matter; NDF=neutral-detergent fiber; ADF=acid-detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid-detergent lignin

Table B10. Body weight (BW) of colobines fed diets 15ADF and 30ADF and digestibility of apparent dry matter and gross energy in those diets.^a

Species	ID	BW (kg)	15ADF			30ADF		
			DM (%)	GE (%)	DE (kcal/g)	DM (%)	GE (%)	DE (kcal/g)
Colobus g. kikuyuensis	Flower	11.34	73.5	73.0	3.26	-	-	-
	Gomez	10.90	80.3	78.5	3.50	78.7	78.0	3.42
	Mean	11.12	76.9	75.8	3.38	78.7	78.0	3.42
	SD	0.31	4.80	3.89	0.17	NA	NA	NA
	Rhett	12.10	76.2	81.6	3.64	73.9	72.5	3.18
Pygathrix n. nemaeus								
Trachypithecus f. francoisi	Jack	7.71	84.6	83.3	3.72	80.0	78.1	3.43
	Janet	5.67	79.7	78.3	3.49	74.4	73.5	3.23
	Chrissie	6.67	82.9	81.7	3.64	77.0	76.4	3.35
	Stanley	3.99	85.9	85.1	3.79	80.1	79.8	3.50
	Fungar	5.75	78.9	77.7	3.47	72.0	70.9	3.11
	GooNgoot	5.85	-	-	-	81.1	80.6	3.54
Colobines	Mean	5.59	65.5	81.2	3.62	77.4	76.6	3.36
	SD	1.38	3.00	3.18	0.14	3.63	3.76	0.17
Colobines	Mean	7.78	80.3	79.9	3.56	77.2	76.2	3.35
	SD	2.94	4.2	3.8	0.17	3.37	3.55	0.16

Table B11. Digesta transit time (TT_1) and total retention time (R_{GIT}) in hours of ruffed lemurs (*Varecia* spp.) fed diet 15ADF.

Species	ID	BW (kg)	Marker type					
			Bead			Co-EDTA		
			TT_1	R_{GIT}	TT_1	R_{GIT}	TT_1	R_{GIT}
<i>Varecia variegata rubra</i>	Athena	4.50	1.5	4.3	1.5	4.5	4.5	2.4
	Michele	4.30	4.5	12.3	7.5	1.1	1.5	5.6
	Rinda	5.30	4.5	4.5	7.5	2.6	4.5	1.9
	Spica	4.95	1.5	5.8	1.5	6.4	1.5	1.2
	Mean	4.76	3.0	6.7	4.50	3.6	3.0	2.8
<i>Varecia variegata variegata</i>	SD	0.45	1.73	3.76	3.46	2.31	1.50	1.96
	Ino	4.65	1.5	1.1	1.5	3.1	1.5	1.1
	Night	5.00	4.5	3.3	1.5	5.5	1.5	8.8
	Mean	4.83	3.0	2.2	1.5	3.4	1.5	5.0
	SD	0.25	2.12	1.53	0.00	2.45	0.00	5.41
<i>Varecia variegata spp</i>	Mean	4.78	3.0	5.2	3.5	3.9	2.5	3.5
	SD	0.37	1.64	3.80	3.10	1.97	1.55	3.07

Table B12. Digesta transit time (TT₁) and total retention time (R_{GIR}) in hours of ruffed lemurs (*Varecia.spp.*) fed diet 30ADF.

Species	ID	BW (kg)	Marker type					
			Acetate Bead		Co-EDTA		Cr-fiber	
			TT ₁	R _{GIR}	TT ₁	R _{GIR}	TT ₁	R _{GIR}
<i>Varecia variegata rubra</i>	Athena	4.05	1.5	4.8	1.5	3.4	1.5	1.4
	Michele	3.70	7.5	8.5	4.5	2.5	4.5	1.4
	Rinda	4.30	1.5	5.5	-	-	-	-
	Spica	4.25	1.5	5.7	1.5	4.1	4.5	2.0
	Mean	4.08	3.0	6.1	2.5	3.3	3.5	1.6
	SD	0.27	3.00	1.63	1.73	0.77	1.73	0.33
<i>Varecia variegata variegata</i>	Ino	4.40	1.5	2.5	1.5	1.1	1.5	3.6
	Night	3.80	1.5	2.1	4.5	1.0	1.5	3.1
	Mean	4.10	1.5	2.3	3.0	1.0	1.5	3.4
	SD	0.42	0.00	0.31	2.12	0.09	0.00	0.37
<i>Varecia variegata ssp.</i>	Mean	4.08	2.5	4.9	2.7	2.4	2.7	2.3
	SD	0.28	2.45	2.35	1.64	1.37	1.64	1.03

Table B13. Digesta transit time (TT₁) and total retention time (R_{GIT}) in hours of howler monkeys (*Alouatta* spp.) fed diet 15ADF.

Species	ID	BW (kg)	Marker type					
			Acetate Bead		Co-EDTA		Cr-fiber	
			TT ₁	R _{GIT}	TT ₁	R _{GIT}	TT ₁	R _{GIT}
<i>Alouatta caraya</i>	Phoebe	4.72	-	-	22.5	20.1	-	-
	Katie	8.94	-	-	22.5	22.3	-	-
	Jessie	7.44	22.5	8.0	7.5	24.7	46.5	8.0
	Shadow	10.66	31.5	33.9	4.5	12.7	28.5	19.9
	Mean	7.94	27.0	20.9	14.3	19.9	37.5	13.9
<i>Alouatta villosa palliata</i>	SD	2.52	6.36	18.30	9.60	5.19	12.73	8.41
	Jalapeno	5.15	19.5	15.4	7.5	28.7	7.5	54.4
	Waldo	6.55	16.5	36.1	7.5	38.5	16.5	21.1
	Mean	5.85	18.0	25.7	7.5	33.6	12.0	37.8
	SD	0.99	2.12	14.66	0.00	6.87	6.36	23.55
<i>Alouatta seniculus sara</i>	Pilgrim	9.15	70.5	34.6	22.5	87.3	46.5	62.6
	Howie	7.50	22.5	34.4	22.5	29.1	22.5	17.2
	Mean	8.32	46.5	34.5	22.5	58.2	34.5	39.9
	SD	1.17	33.94	0.11	0.00	41.15	16.97	32.10
<i>Alouatta spp</i>	Mean	7.51	30.5	27.1	14.6	32.9	28.0	30.5
	SD	2.03	20.20	12.15	8.48	23.22	15.92	22.3

Table B14. Digesta transit time (TT₁) and total retention time (R_{GIT}) in hours of howler monkeys (*Alouatta* spp.) fed diet 30ADF.

Species	ID	BW (kg)	Marker type					
			Bead		Co-EDTA		Cr-fiber	
			TT ₁	R _{GIT}	TT ₁	R _{GIT}	TT ₁	R _{GIT}
<i>Alouatta caraya</i>	Phoebe	4.72	19.5	8.0	7.5	27.8	19.5	41.5
	Katie	8.94	10.5	17.0	4.5	29.3	46.5	10.8
	Shadow	10.66	-	-	16.5	58.1	-	-
	Mean	8.10	15.0	12.5	9.5	38.4	33.0	26.1
	SD	3.06	6.36	6.36	6.24	17.08	19.09	27.71
<i>Alouatta villosa palliata</i>	Jalapeno	6.05	7.5	25.3	4.5	33.3	4.5	35.8
	Waldo	6.85	19.5	25.5	10.5	27.9	4.5	37.8
	Mean	6.45	13.5	25.4	7.5	30.6	4.5	36.8
	SD	0.57	8.49	0.14	4.24	3.82	0.00	1.41
<i>Alouatta seniculus sara</i>	Pilgrim	8.55	46.5	32.0	46.5	82.0	28.5	69.5
	Howie	7.50	25.5	13.9	22.5	24.6	25.5	12.2
	Mean	8.03	36.0	22.9	34.5	53.3	27.0	40.8
	SD	0.74	14.85	12.80	16.97	40.59	2.12	40.52
<i>Alouatta</i> sp.	Mean	7.61	21.5	20.3	16.1	40.4	21.5	34.6
	SD	1.97	13.90	8.86	14.94	21.53	15.95	21.66

Table B15. Digesta transit time (TT₁) and total retention time (R_{GIR}) in hours of colobine primates fed diet 15ADF.

Species	ID	BW (kg)	Marker type					
			Bead		Co-EDTA		Cr-fiber	
			TT ₁	R _{GIR}	TT ₁	R _{GIR}	TT ₁	R _{GIR}
<i>Colobus guereza kikuyuensis</i>	Flower	11.34	-	-	28.5	41.2	-	-
	Gomez	10.90	31.5	20.7	43.5	46.9	46.5	37.6
	Mean	11.12	31.5	20.7	36.0	44.0	46.5	37.6
	SD	0.31	NA	NA	10.6	4.0	NA	NA
	Rhett	12.10	31.5	-	1.5	35.3	1.5	33.8
<i>Pygathrix nemaeus nemaeus</i>	Janet	5.67	31.5	44.9	10.5	37.7	31.5	22.3
	Chrissie	6.67	22.5	48.4	10.5	50.6	22.5	38.8
	Stanley	3.99	-	-	22.5	39.2	-	-
	Fungar	5.75	-	-	10.5	37.0	-	-
	Mean	5.96	27.0	46.7	13.5	41.1	27.0	30.5
<i>Trachypithecus francoisi francoisi</i>	SD	1.38	6.36	2.48	6.00	6.38	6.36	11.65
	Mean	8.02	29.3	38.0	18.2	41.1	25.5	33.1
	SD	3.04	4.50	15.08	14.27	5.62	18.81	7.52
	Mean	8.02	29.3	38.0	18.2	41.1	25.5	33.1
	SD	3.04	4.50	15.08	14.27	5.62	18.81	7.52

Table B16. Digesta transit time (TT₁) and total retention time (R_{GIR}) in hours of colobines fed diet 30 ADF.

Species	ID	BW (kg)	Marker type					
			Bead		Co-EDTA		Cr-fiber	
			TT ₁	R _{GIR}	TT ₁	R _{GIR}	TT ₁	R _{GIR}
<i>Colobus guereza kikuyuensis</i>	Gomez	10.70	31.5	37.6	43.5	53.4	43.5	68.6
<i>Pygathrix nemaeus nemaeus</i>	Rhett	11.75	43.5	-	19.5	32.5	-	-
<i>Trachypithecus francoisi francoisi</i>	Jack	7.78	22.5	17.4	10.5	36.6	-	-
	Janet	5.72	-	-	19.5	27.3	-	-
	Chrissie	5.76	-	-	19.5	40.5	-	-
	Stanley	3.77	19.5	15.6	4.5	47.8	10.5	42.5
	Fungar	6.75	28.5	95.7	19.5	28.6	-	-
	Goo Ngoot	5.85	43.5	42.7	19.5	32.5	19.5	35.6
	Mean	5.94	28.5	42.8	15.5	35.5	15.0	39.0
	SD	1.33	10.68	37.34	6.48	7.76	6.36	4.85
Colobines	Mean	7.26	31.8	41.8	19.5	37.4	24.5	48.9
	SD	2.71	10.58	32.42	11.22	9.27	17.06	17.41

Table B17. Body weight (BW) and dry matter intake (DMI) of two cercopithecine monkeys fed diet 15ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a				
				DM	NDF	ADF	C	HC ADL
<i>Cercocebus g. chrysogaster</i>	Heine	9.6	23.8	85.7	76.5	75.7	75.4	77.9 81.5
<i>Mandrillus l. leucophaeus</i>	Susie	10.20	11.7	85.6	76.1	83.2	77.4	77.5 82.1

DM=dry matter; NDF=neutral detergent fiber; ADF=acid detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid detergent lignin.

Table B18. Body weight (BW) and dry matter intake (DMI) of two cercopithecine monkeys fed diet 30ADF and apparent digestibility of dry matter (DM) and fiber fractions in that diet.

Species	ID	BW (kg)	DMI (g/kg BW)	Digestibility (%) of ^a				
				DM	NDF	ADF	C	HC ADL
<i>Cercocebus g. chrysogaster</i>	Heine	10.10	23.5	82.0	80.5	78.0	78.7	86.0 70.7
<i>Mandrillus l. leucophaeus</i>	Susie	10.00	7.2	81.1	79.2	79.0	77.6	84.9 46.2

DM=dry matter; NDF=neutral detergent fiber; ADF=acid detergent fiber; C=cellulose; HC=hemicellulose; ADL=acid detergent lignin.

Table B19. Body weight (BW) of two cercopithecine monkeys fed diets 15ADF and 30ADF and the apparent digestibility of dry matter and gross energy in those diets.*

Species	ID	BW (kg)	15ADF			30ADF		
			DM (%)	GE (%)	DE (kcal/g)	DM (%)	GE (%)	DE (kcal/g)
<i>Cercocebus g. chrysogaster</i>	Heine	9.60	85.7	89.1	3.97	82.0	82.5	3.62
<i>Mandrillus l. leucophaeus</i>	Susie	10.20	85.6	83.7	3.73	81.1	78.9	3.46

*DM=dry matter; GE=gross energy; DE=digestible energy

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