

# Effect of Dietary Fiber Concentration on Apparent Digestibility and Digesta Passage in Non-human Primates. II. Hindgut- and Foregut-Fermenting Folivores

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Two test diets with different acid detergent fiber (ADF) concentrations (15% ADF, 30% ADF) were fed to seven adult hindgut- and seven adult foregut-fermenting primates. Apparent digestibilities (%) of dietary dry matter (DM), gross energy (GE), and fiber components (neutral detergent fiber [NDF], ADF, hemicellulose [HC], and cellulose [C]) were measured. Rates of digesta transit (TT1) and retention (RGIT) times were assessed using acetate beads, Co-ethylenediaminetetraacetic acid, and Cr-mordanted fiber as markers. Apparent digestibilities (%) of components of the 15ADF and 30ADF diets, respectively, by hindgut versus foregut fermenters were 69.3 and 61.7 versus 81.2 and 76.7 for DM, 68.5 and 61.5 versus 80.9 and 75.6 for GE, and 44.8 and 47.4 versus 77.1 and 74.7 for NDF. No significant differences in TT1 or RGIT between dietary treatments or markers were detected. The role of plant fiber in maintaining the health and normal function of the gastrointestinal tract in captive leaf-eating primates is discussed. Zoo Biol 18:537–549, 1999. © 1999 Wiley-Liss, Inc.

**Key words:** *Alouatta*; *Trachypithecus*; *Pygathrix*; nutrition; colobinae; howler monkeys; food intake; transit time; retention time

## INTRODUCTION

Within the order Primates, there are many species whose diet consists, in part or entirely, of leaf material [Oftedal, 1991]. Variations in feeding habits among these leaf eaters are related to differences in gastrointestinal tract morphology [Oftedal,

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1991; Chivers, 1994]. In colobinae, microbial fermentation of consumed plant material occurs in the large, sacculated forestomach [Bauchop and Martucci, 1968] and in howlers in the sacculated cecum and/or colon [Milton and McBee, 1983; Ullrey, 1986]. The sites of microbial fermentation and nutrient absorption differ between colobinae and howlers relative to the site of gastric digestion, and this difference affects the rate and extent of nutrient extraction and undoubtedly influences life history, including selection of the natural diet within the chosen habitat [Shipley et al., 1998].

## METHODS

As part of a larger study of the digestive capabilities of non-human primates [Edwards and Ullrey, 1999], seven individually housed adult howler monkeys (two red howlers [*Alouatta seniculus seniculus*], two mantled howlers [*Alouatta villosa palliata*], and three black howlers [*Alouatta caraya*]), and seven individually housed colobine primates (one Kikuyu colobus [*Colobus guereza kikuyuensis*], one Northern douc langur [*Pygathrix nemaeus nemaeus*], and five Francois langurs [*Trachypithecus francoisi francoisi*]) were included in four separate experiments. All animals were in good health throughout the study. The experimental protocol was coordinated within the established routines of daily animal care and enclosure maintenance. In each experiment, a crossover design was used so that each animal's response was measured for each of two diets. Body weights were collected at the onset of the first trial, during the crossover transition to the second trial, and at the completion of the second trial. Although the intention was to allow all individuals to remain in the study until completion, some individuals were removed from the study before the final collection for reasons unrelated to the experimental treatments.

Two extruded test diets, each from a single manufactured lot, were offered ad libitum, as 100% of the daily ration during the trials. Fiber concentration was the primary variable of the two test diets. Both diets were formulated to meet or exceed the nutrient requirements of non-human primates [NRC, 1978]. The ingredients and calculated nutrient composition of the two test diets, designated as 15ADF and 30ADF, are provided in Tables 1 and 2, respectively.

In vivo apparent digestibilities of dry matter (DM), fiber fractions (neutral detergent fiber [NDF], acid detergent fiber [ADF], cellulose [C], and hemicellulose [HC]), and gross energy (GE) were measured for the two test diets. Test subjects were gradually transferred from their standard mixed diet of primate biscuits, fruits, and vegetables to the test diet as their sole nutrient source. Food intake was measured daily to ensure that ad libitum quantities of the test diets were offered. After a 7-day adaptation period to the test diets, a 14-day period of total fecal collection was employed. Composites of daily fecal samples and test diets were analyzed for DM, GE [AOAC, 1990], and sequential NDF, ADF, and acid detergent lignin (ADL) [Goering and Van Soest, 1970]. HC was determined as the difference between NDF and ADF. C was determined as the difference between ADF and ADL.

Rates of digesta passage and digesta retention time were evaluated in each individual, using 1-mm acetate beads, Na Co-ethylenediaminetetraacetic acid (EDTA) and Cr-mordanted fiber as markers during consumption of each of the test diets. Na Co-EDTA and Cr-mordanted fiber were prepared using methods described by Udén [1978]. The markers were mixed with ground test diet ( $\leq 20$  g) and fruit nectar ( $\leq 25$  g) to enhance palatability. The fruit nectar also provided moisture sufficient to hold

## Fiber Levels, Digestibility, and Digesta Passage. II. Folivores 539

**TABLE 1. Composition of the lower (15ADF) and higher fiber (30ADF) test diets**

Ingredient	Percentage by weight <sup>a</sup>	
	15ADF	30ADF
Soybean meal (44%)	13	5
Corn gluten meal	11	15
Corn grain	24	—
Sugar beet pulp	5	5
Soybean hulls	19.762	52.762
Corn hominy feed	10	5
Sucrose	10	10
Soybean oil	3	3
Dicalcium phosphate	1.85	2.2
Calcium carbonate	0.8	0.45
L-Lysine (78%)	0.3	0.3
Sodium chloride	0.5	0.5
Vitamin trace mineral premix	0.5	0.5
Mono prop mold inhibitor	0.1	0.1
Red cabbage extract (coloration)	0.1	0.1
Vitamin C (ethocel coated)	0.05	0.05
Feed flavor	0.038	0.038

<sup>a</sup>Air-dry basis.

<sup>b</sup>Formulated to provide per kilogram of diet: 8,000 IU vitamin A, 1,750 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 mg vitamin B12, 200 mg choline, 25 mg Fe, 10 mg Cu, 90 mg Zn, 45 mg Mn, 1 mg I, 0.23 mg Se.

<sup>c</sup>MonoProp (50% propionic acid on verxite), Anitox Corporation, Bulford, GA.

the marker/test diet mixture together. The dough-like mixture was rolled into balls and hand-fed to each subject.

Acetate bead markers were offered in quantities of 110 pieces. The first appearance of these markers in the feces corresponded with the beginning of fecal collection for digestibility trials. Na Co-EDTA (14.35% Co) was dosed orally at 0.50 g per individual, providing 71.75 mg Co as a marker of the liquid phase of digesta. Cr-mordanted fiber was fed in quantities to deliver 40 mg Cr to the test subject as a particulate digesta marker.

Markers were fed in a single-pulse bolus to each individual between 0900 and 1000 hours. After the introduction of the marker, all feces were collected at 3-hour

**TABLE 2. Calculated nutrient composition of the lower (15ADF) and higher fiber (30ADF) test diets (all expressed on dry matter basis, except moisture)**

Nutrient	Diet	
	15ADF	30ADF
Moisture (%)	8.8	8.3
Gross energy (kcal/g)	4.80	4.69
Crude protein (%)	20.51	19.95
Lysine (%)	1.11	1.02
Ether extract (crude fat) (%)	5.90	5.19
Neutral detergent fiber (%)	23.98	41.93
Acid detergent fiber (%)	15.04	29.59
Calcium (%)	1.02	1.08
Phosphorus (%)	0.70	0.70

intervals. Post-dusk and pre-dawn samples were collected at 2100 and 0300 hours, respectively. Samples were not collected or monitored at 0000 hours to prevent disruption of the animals during the night. The collection schedule continued for 14 days after the introduction of each marker bolus.

Acetate bead markers were recovered from fresh fecal samples by manual separation. Samples collected during the chemical marker trials were digested with nitric-perchloric acid [Fenton and Fenton, 1979] and analyzed using atomic absorption/emission spectrophotometry.

The mean retention time ( $R_{GIT} + TT_1$ ) was calculated as previously described [Edwards and Ullrey, 1999]. Transit time ( $TT_1$ ) was determined as the time between dosing and first appearance of the marker in the feces. Total retention time ( $R_{GIT}$ ) was determined by subtracting  $TT_1$  from mean retention time. Statistical comparisons of response criteria between diets were made using paired *t*-tests.

## RESULTS

There were no statistical differences ( $P > 0.05$ ) among the body masses of the two groups, hindgut fermenters (*Alouatta* spp) and foregut fermenters (colobine primates), fed diets 15ADF or 30ADF (Table 3).

DM intake was expressed as grams of DM consumed per day (24 hours) and as a function of the animal's body mass (g/kg BM or %BM). There were no differences ( $P > 0.05$ ) between the DM intakes of either diet by *Alouatta* spp or the colobine species (Table 3).

The apparent DM digestibility of diet 30ADF by colobine species was lower ( $P < 0.05$ ) than that of diet 15ADF. The apparent DM digestibility of diet 30ADF by *Alouatta* spp was also lower ( $P < 0.01$ ) than that of diet 15ADF. Statistical

**TABLE 3. Mean body weight (BW) and mean dry matter intake (DMI) of primates fed diets 15ADF and 30ADF grouped by species and gastrointestinal tract type**

Species	Diet	<i>n</i>	BW (kg)	DMI (g/d)	DMI (g/kg BW)	DMI (% BW)
<i>Alouatta caraya</i>	15ADF	3	8.11 ± 3.06	128.0 ± 23.1	17.6 ± 7.2	1.76 ± 0.72
	30ADF	3	8.11 ± 3.06	185.1 ± 20.3	25.5 ± 11.2	2.55 ± 1.12
<i>Alouatta villosa palliata</i>	15ADF	2	5.85 ± 0.99	141.0 ± 41.4	23.9 ± 3.0	2.39 ± 0.30
	30ADF	2	6.45 ± 0.57	131.5 ± 28.7	20.3 ± 2.7	2.03 ± 0.27
<i>Alouatta seniculus sara</i>	15ADF	2	8.33 ± 1.17	130.6 ± 32.2	16.1 ± 6.1	1.68 ± 0.17
	30ADF	2	8.03 ± 0.74	157.7 ± 7.0	19.7 ± 1.0	1.79 ± 0.27
Hindgut fermenters	15ADF	7	7.52 ± 2.20	132.4 ± 25.9	18.9 ± 6.1	1.89 ± 0.57
	30ADF	7	7.61 ± 1.97	161.9 ± 29.4	22.4 ± 7.2	2.24 ± 0.73
<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 nemaus nemaus</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 ± 1.38	182.4 ± 29.6	31.6 ± 7.7	3.16 ± 0.86
	30ADF	5	5.96 ± 1.49	176.6 ± 55.0	30.5 ± 9.3	3.05 ± 1.03
Foregut fermenters	15ADF	7	7.54 ± 2.95	213.7 ± 98.5	29.7 ± 9.4	2.97 ± 0.94
	30ADF	7	7.46 ± 2.86	204.0 ± 94.3	28.6 ± 9.9	2.86 ± 0.99

<sup>a,b</sup>Values in same column with different superscripts differ ( $P < 0.01$ ).

<sup>c,d</sup>Values in same column with different superscripts differ ( $P < 0.05$ ).

## Fiber Levels, Digestibility, and Digesta Passage. II. Folivores 541

differences were observed in apparent DM digestibility between gastrointestinal tract type (hindgut vs. foregut), within either diet 15ADF or 30ADF ( $P < 0.0005$ ) (Table 4).

The apparently digestible energy (DE) of diet 30ADF was lower ( $P < 0.01$ ) than that of diet 15ADF for both the colobine species and *Alouatta* spp (Table 4).

No statistical differences were seen in the digestibility of the individual cell wall components (NDF, ADF, C, HC) 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 5).

There was no statistical difference seen in either  $TT_1$  (Table 6) or  $R_{GIT}$  (Table 7) between diets 15ADF and 30ADF for acetate bead markers, Co-EDTA, and Cr-mordanted fiber fed to *Alouatta* spp or the colobine species. Unfortunately, owing to previously mentioned circumstances, eight animals had to be removed from the second Cr-mordanted fiber trial, thus eliminating them from the statistical analyses. There were no statistical differences seen in either  $TT_1$  (Table 6) or  $R_{GIT}$  (Table 7) between the two test diets for acetate beads, Na Co-EDTA, or Cr-mordanted fiber. Markers (acetate bead, Co-EDTA, and Cr-mordanted fiber) were compared with each other to determine the level of correlation for the items 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

The gastrointestinal and dietary adaptations that are well known in domestic herbivores also are seen in leaf-eating primates. Digestive efficiencies of hindgut

**TABLE 4. Mean apparent dry matter digestibility (DMD), digestible energy (DE) of diets 15ADF and 30ADF, and digestible energy intake (DEI) primates groups by species and gastrointestinal tract type**

Species	Diet	<i>n</i>	DMD (%)	DE (%)	DE (kcal/g)	DEI (kcal/kg.75)
<i>Alouatta caraya</i>	15ADF	3	67.7 ± 3.1	66.4 ± 3.3	2.96 ± 0.15	83.70 ± 22.98
	30ADF	3	62.0 ± 1.5	61.6 ± 2.5	2.70 ± 0.11	111.33 ± 34.00
<i>Alouatta villosa palliata</i>	15ADF	2	70.0 ± 0.9	68.8 ± 0.3	3.07 ± 0.01	114.07 ± 19.87
	30ADF	2	62.1 ± 0.7	61.8 ± 0.1	2.71 ± 0.00	87.76 ± 13.53
<i>Alouatta seniculus sara</i>	15ADF	2	71.0 ± 8.1	71.5 ± 8.2	3.19 ± 0.37	84.86 ± 19.88
	30ADF	2	60.7 ± 0.5	61.1 ± 0.9	2.68 ± 0.04	88.76 ± 1.00
Hindgut fermenters	15ADF	7	69.3 ± 4.1 <sup>a,e</sup>	68.5 ± 4.5 <sup>a</sup>	3.06 ± 0.18	92.71 ± 22.82
	30ADF	7	61.7 ± 1.1 <sup>b,c</sup>	61.5 ± 1.5 <sup>b</sup>	2.70 ± 0.07	98.14 ± 23.83
<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 nemaus nemaus</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 ± 3.0	81.2 ± 3.2	3.62 ± 0.14	176.97 ± 37.23
	30ADF	5	76.7 ± 3.5	75.7 ± 3.6	3.32 ± 0.15	156.35 ± 44.35
Foregut fermenters	15ADF	7	81.2 ± 3.4 <sup>c,f</sup>	80.9 ± 2.8 <sup>c</sup>	3.61 ± 0.13	173.73 ± 53.36
	30ADF	7	76.6 ± 3.2 <sup>d,f</sup>	75.6 ± 3.3 <sup>d</sup>	3.32 ± 0.15	152.41 ± 48.07

<sup>a,b</sup>Values in same column with different superscripts differ ( $P < 0.01$ ).

<sup>c,d</sup>Values in same column with different superscripts differ ( $P < 0.01$ ).

<sup>e,f</sup>Values in same column with different superscripts differ ( $P < 0.0001$ ).

**TABLE 5. Mean digestibility (%) of various fiber components (NDF, ADF, C, HC) in diets 15ADF and 30ADF for primates grouped by species and gastrointestinal tract type**

Species	Diet	<i>n</i>	NDF	ADF	C	HC
<i>Alouatta caraya</i>	15ADF	3	46.5 ± 9.6	40.5 ± 12.5	38.0 ± 10.8	53.6 ± 8.8
	30ADF	3	45.8 ± 4.7	37.7 ± 4.9	36.8 ± 5.3	63.6 ± 5.9
<i>Alouatta villosa palliata</i>	15ADF	2	43.7 ± 5.1	43.8 ± 3.0	39.6 ± 4.2	51.8 ± 3.5
	30ADF	2	52.6 ± 4.7	46.2 ± 5.7	44.5 ± 8.4	66.8 ± 2.6
<i>Alouatta seniculus sara</i>	15ADF	2	43.4 ± 14.4	43.1 ± 19.2	40.8 ± 23.6	43.8 ± 6.8
	30ADF	2	44.8 ± 3.2	39.5 ± 5.9	37.3 ± 7.3	56.4 ± 2.7
Hindgut fermenters	15ADF	7	44.8 ± 8.5	42.2 ± 10.8	39.2 ± 11.7	50.3 ± 6.1 <sup>a</sup>
	30ADF	7	47.4 ± 5.0	40.6 ± 5.8	39.1 ± 6.6	62.4 ± 6.0 <sup>b</sup>
<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 ± 5.3	82.3 ± 4.8	84.3 ± 7.0	73.7 ± 7.2
	30ADF	5	75.7 ± 7.7	76.9 ± 12.8	76.9 ± 12.8	77.3 ± 3.0
Foregut fermenters	15ADF	7	77.1 ± 6.4	79.7 ± 7.0	80.4 ± 10.8	71.9 ± 6.7
	30ADF	7	74.7 ± 6.7	72.6 ± 13.2	75.2 ± 11.2	77.0 ± 2.7

<sup>a,b</sup>Values in same column with different superscripts differ ( $P < 0.01$ ).

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

Colobines (black and white colobus, Francois' langur, douc langur) exhibit the most extensive gastrointestinal modifications in primates for microbial fermentation

**TABLE 6. Mean transit time (TT<sub>1</sub>, hours) of various markers, acetate beads, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primates grouped by species and gastrointestinal tract type**

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
<i>Alouatta caraya</i>	15ADF	—	16.5 ± 10.4(3) <sup>a</sup>	—
	30ADF	—	9.5 ± 6.2(3)	—
<i>Alouatta villosa palliata</i>	15ADF	18.0 ± 2.2(2)	7.5 ± 0.0(2)	12.0 ± 6.4(2)
	30ADF	13.5 ± 8.5(2)	7.5 ± 4.24(2)	4.5 ± 0.0(2)
<i>Alouatta seniculus sara</i>	15ADF	46.5 ± 33.9(2)	22.5 ± 0.0(2)	34.5 ± 17.0(2)
	30ADF	36.0 ± 14.8(2)	34.5 ± 17.0(2)	27.0 ± 2.1(2)
Hindgut fermenters	15ADF	32.3 ± 25.6(4)	15.6 ± 8.6(7)	23.3 ± 16.7(4)
	30ADF	24.8 ± 16.3(4)	16.1 ± 14.9(7)	15.8 ± 13.0(4)
<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 ± 6.0(4)	—
	30ADF	—	15.8 ± 7.5(4)	—
Foregut fermenters	15ADF	31.5 ± 0.0 (2)	16.5 ± 14.8(6)	46.5(1)
	30ADF	37.5 ± 8.5 (2)	21.0 ± 12.5(6)	43.5(1)

<sup>a</sup>*n* in parentheses.

## Fiber Levels, Digestibility, and Digesta Passage. II. Folivores 543

**TABLE 7. Mean retention time ( $R_{GIT}$ , hours) of various markers, acetate beads, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for primates grouped by species and gastrointestinal tract type**

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
<i>Alouatta caraya</i>	15ADF	—	18.4 ± 5.0(3) <sup>a</sup>	—
	30ADF	—	38.4 ± 17.1(3)	—
<i>Alouatta villosa palliata</i>	15ADF	25.7 ± 14.6(2)	33.6 ± 6.9(2)	37.8 ± 23.6(2)
	30ADF	25.4 ± 0.1(2)	30.6 ± 3.8(2)	36.8 ± 1.4(2)
<i>Alouatta seniculus sara</i>	15ADF	34.5 ± 0.1(2)	58.2 ± 41.2(2)	39.9 ± 32.1(2)
	30ADF	22.9 ± 12.8(2)	53.3 ± 40.6(2)	40.8 ± 40.5(2)
Hindgut fermenters	15ADF	30.1 ± 9.9(4)	34.1 ± 24.8(7)	38.8 ± 23.0(4)
	30ADF	24.2 ± 7.5(4)	40.4 ± 21.5(7)	38.8 ± 23.5(4)
<i>Colobus guereza kikuyuensis</i>	15ADF	30.7(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 ± 6.4(4)	—
	30ADF	—	36.1 ± 9.8(4)	—
Foregut fermenters	15ADF	30.7(1)	41.1 ± 6.2(6)	37.6(1)
	30ADF	37.6(1)	38.4 ± 10.7(6)	68.6(1)

<sup>a</sup>*n* in parentheses.

of plant cell wall. Although feeding habits are diverse among these species, foregut fermentation is present throughout the sub-family. As a result, regardless of the type of plant material consumed, that food is subjected to fermentative processes.

### Food Intake

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. Owing in part to its effect on gut fill, plant cell wall is also important as a negative regulator of intake [Van Soest, 1982]. However, reduction of fiber particle size by grinding, as was the case in this study, may minimize the gut fill effect.

DM intakes of both diets 15ADF and 30ADF, 1.42% and 1.44% of body mass, 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% vs. 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 DM intakes, 154.8 g/day of 15ADF and 153.8 g/day of 30ADF, which were not statistically different between the two dietary treatments, were similar to those reported in other studies with *Colobus* (159 g/day [Oftedal et al., 1982] and 158 g/day [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, differences in the body mass and body composition of study subjects, or a function of the limited sample size available in all three studies.

Dierenfeld et al. [1992] found that mean DM 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 DM as a percentage of body mass (2.97% of 15ADF, 2.86% of 30ADF) with no significant differences between dietary treatments.

The single douc langur, which was the heaviest animal (11.9 kg) included in the study, had the highest level of DM intake as a percentage of body mass (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 an average gastrointestinal volume, and although the proboscis monkey had a very high functional absorptive area, the potential fermenting volume was low.

### Digestibility

Microbial fermentation of 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 factors such as diet composition, rate of digestion, and level of intake [Allen and Mertens, 1988; Church, 1988]. The effect of level 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, DM digestibility is depressed as a consequence of an increased rate of digesta passage through the gut. The depression in digestibility related to increased intake is not limited to fiber but also includes more readily fermentable components of the diet, such as starch.

It is apparent that these factors are closely inter-related and dependent on 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 drawing comparisons between the digestive capabilities of foregut and hindgut fermenters have been published [Hintz, 1969; Olsson, 1969; Parra, 1978], their conclusions were limited by the previously described variables. However, the reviewers suggested that the fiber-digesting capabilities of non-ruminant herbivores are commonly less than those of ruminants.

The results of this study demonstrate that howler monkeys possess the capability of digesting and utilizing fibrous feeds, but the apparent DM digestibilities 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 apparent DM digestibility 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 apparent DM digestibility when consuming diet 30ADF versus diet 15ADF.

DM 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

## Fiber Levels, Digestibility, and Digesta Passage. II. Folivores 545

al. [1982, unpublished] also reported DM digestibilities as high as 90% in silvered leaf monkeys (*Semnopithecus crisatus*) fed a mixed diet without browse plant supplementation. This higher level of DM 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.

Sakaguchi et al. [1991] found the DM digestibility of a manufactured (“cubed”) diet (16.4% ADF, DM basis) fed to silvered leaf monkeys was 75.7%. This value is lower but comparable with the results of the present study. Francois’ langurs, a closely related species, digested 82.4% of the DM in diet 15ADF. The douc langur included in this study exhibited DM digestibilities of 76.2% and 73.9%, for diets 15ADF and 30ADF, respectively. These values were consistently lower in this study than for other colobines (*Colobus*, *Trachypithecus*) maintained on the same diets. These values were the lowest apparent DM digestibility estimates reported for a colobine primate. However, owing to the limited sample size for this species (n = 1), further study is warranted.

The significantly lower apparent DM digestibility 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. Apparent DM digestibilities of mixed diets in other studies, including those containing browse plants, were not dramatically lower than those seen in this study.

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]. 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 consisted of “processed” fiber particles.

Howler monkeys digested relatively more of the HC fraction of both diets 15ADF and 30ADF than the C fraction compared with digestion of those components by the foregut fermenters. This has been observed in studies of HC 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 depends on the removal of C that surrounds it. It is possible that some linkages that 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.

Fiber component digestibility exhibited by the colobines demonstrates that these species are suited to consume a diet containing higher concentrations of plant cell wall. 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, relative to those digestibilities in diet 15ADF. Interestingly, as seen in the hindgut-fermenting howlers, HC digestibility was numerically higher in diet 30ADF (77.0%) than in diet 15ADF (71.9%).

Similar but numerically lower apparent 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, and 87.8–89.1% C [Dierenfeld et al., 1992]. These results support Chivers' [1994] characterization of the proboscis monkey, the largest colobine included in his study, but possessing the smallest stomach and largest large intestine. He proposed that this anatomical arrangement results in a low fermenting ability and high absorbing ability. This is further supported by studies of natural foraging behavior, 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 relative contributions of microbial fermentation in the proboscis hindgut were not examined.

Herbivores with foregut fermentation are more efficient in their ability to digest plant fiber owing 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]. The digestible energy estimates reported by Ullrey et al. [unpublished, 1982] are comparable with those seen in this study, when the differences in test diet are considered. Digestible energy estimates were not reported by any other authors.

When compared with primates apparently lacking specific gastrointestinal modifications to support significant microbial populations (e.g., *Varecia* spp [Edwards and Ullrey, 1999]), both hindgut- and foregut-fermenting primates have an increased ability to digest the dietary DM of diets 15ADF and 30ADF ( $P < 0.0001$ ) (Table 8).

### Digesta Passage and Retention

Digesta transit time in herbivores, when compared across dietary and gastrointestinal types, tends to decrease from ruminants to non-ruminants with hindgut fermentation to more generalist feeders (e.g., omnivores). The rate of passage in herbivores tends to increase with decreasing body size [Parra, 1978]. It is generally believed

**TABLE 8. Mean apparent dry matter digestibility (DMD), digestible energy (DE) of diets 15ADF and 30ADF, and digestible energy intake (DEI) for primates grouped by gastrointestinal tract (GIT) type**

GIT type species	Diet	<i>n</i>	DMD (%)	DE (%)	DE (kcal/g)
Simple GIT					
<i>Varecia variegata</i> spp	15ADF	5	51.0 ± 4.7 <sup>a,c</sup>	47.0 ± 5.8	2.20 ± 0.29
	30ADF	5	41.7 ± 6.0 <sup>b,e</sup>	39.7 ± 7.4	1.74 ± 0.30
Hindgut fermenter					
<i>Alouatta</i> spp 1	5ADF	7	69.3 ± 4.1 <sup>c,f</sup>	68.5 ± 4.5 <sup>c</sup>	3.06 ± 0.18
	30ADF	7	61.7 ± 1.1 <sup>d,f</sup>	61.5 ± 1.5 <sup>d</sup>	2.70 ± 0.07
Foregut fermenter					
<i>Colobus</i> , <i>Pygathrix</i> , <i>Trachypithecus</i>	15ADF	7	81.2 ± 3.4 <sup>c,g</sup>	80.9 ± 2.8 <sup>c</sup>	3.61 ± 0.13
	30ADF	7	76.6 ± 3.2 <sup>d,g</sup>	75.6 ± 3.3 <sup>d</sup>	3.32 ± 0.15

<sup>a,b</sup>Values in same column with different superscripts differ ( $P < 0.05$ ).

<sup>c,d</sup>Values in same column with different superscripts differ ( $P < 0.01$ ).

<sup>e,f,g</sup>Values in same column with different superscripts differ ( $P < 0.0001$ ).

## Fiber Levels, Digestibility, and Digesta Passage. II. Folivores 547

that non-ruminant herbivores exhibit a faster rate of passage and a shorter mean retention time compared with foregut fermenters (ruminants [Moir, 1968; Parra, 1978; Shipley et al., 1998]). These trends were not consistently exhibited in this study.

Estimates of digesta transit times reported here are comparable with two previous studies examining these measures in *Alouatta* spp [Milton, 1981; Crissey et al., 1989]. Although not statistically significant,  $TT_1$  was numerically more rapid for Co- EDTA and slower for Cr-mordanted fiber when the howlers were fed 15ADF than when fed 30ADF. With acetate beads,  $TT_1$  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 hours) [Crissey et al., 1989] was significantly longer than those reported here (24.2 -38.8 hours). 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.

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 mass ( $BM^{0.75}$ ). 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 on 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 hours and a  $R_{GIT}$  of 49 hours. 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 with those determined with Francois' langurs were reported with silvered leaf monkeys fed a higher fiber "cubed" diet using like markers. The rates of passage ( $TT_1$ ) determined with Cr-mordanted fiber were slower and retention times ( $R_{GIT}$ ) shorter in this species when compared with the silvered leaf monkey.

### Implications for Captive Management

Fiber concentrations offered the study subjects in these trials were based on fiber levels consumed by free-ranging primates [Edwards, 1995], yet are higher than those traditionally used in captive diets for these species. In fact, the 15ADF test diet is comparable with the highest fiber, commercially available primate diets that are marketed for specialized folivorous primates. This discrepancy may be due, in part, to the lack of information regarding the fiber intake of free-ranging primates or of the digestive capabilities of these specialized feeders, or the "negative feed factor" connotation often associated with plant fiber. The beneficial role of plant fiber regarding satiety, fecal consistency, and overall gastrointestinal health has been well documented [Cummings, 1978].

Primates with either hindgut or foregut fermentation, subjected to thousands of years of evolutionary pressure, have developed mechanisms to utilize readily available plant foods and effectively degrade plant fiber, yielding significant amounts of energy through symbiotic relationships with gut microorganisms. The unfortunate consequences of presenting rapidly fermentable foods (e.g., commercial fruits and vegetables) to these primates are reported in much of the literature concerned with their captive husbandry [Bauchop and Martucci, 1968; Janssen, 1994]. 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 of comparable importance to “true” nutrients when formulating diets for herbivorous primates.

## CONCLUSIONS

1. Although both groups digest plant fiber effectively, the digestive efficiencies of hindgut fermenters are significantly less than those of foregut fermenters.

2. Increased retention times and reduced rates of passage are observed in leaf-eating primates with adaptations for either hindgut or foregut fermentation.

3. Maintaining plant fiber in the captive diets of these specialized primates at 15% ADF (DM basis), while minimizing presentation of readily fermentable carbohydrates (e.g., starch, sugars), is recommended to promote normal microbial fermentation and gastrointestinal function.

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