Zoo Biology 18:529–536 (1999)

Effect of Dietary Fiber Concentration on Apparent Digestibility and Digesta Passage in Non-human Primates. I. Ruffed Lemurs (*Varecia variegata variegata* and *V. v. rubra*)

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Two test diets with different fiber concentrations (15% acid detergent fiber [ADF], 30% ADF) were fed to five adult female ruffed lemurs (*Varecia variegata*). Apparent digestibility (%) of 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 (TT_1) and retention time (R_{GIT}) were assessed using acetate beads, Co-ethylenediaminetetraacetic acid and Cr-mordanted fiber. Apparent digestibilities (%) of components of the 15ADF and 30ADF diets, respectively, were 51.0 and 41.7 for DM, 47.0 and 39.7 for GE, and 20.4 and 20.7 for NDF. TT_1 was approximately 2.7 hours. R_{GIT} was 3.8 hours. No differences in TT_1 or R_{GIT} between dietary treatments or marker types were detected. Results of this study support anecdotal observations that *Varecia variegata* have a limited capacity to utilize plant cell wall constituents as a significant energy source, when compared with more folivorous prosimans. Zoo Biol 18:529–536, 1999. © 1999 Wiley-Liss, Inc.

Key words: prosimian; nutrition; food intake; transit time; retention time

INTRODUCTION

Varecia variegata has been described as frugivorous [Petter et al., 1977; White, 1989], a feeding strategy that is in agreement with inferences from their dental morphology [Tattersall, 1982]. Although the majority (81.6%) of food items selected by free-ranging individuals appears to be those that would be considered "more digest-

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Received for publication April 3, 1999; Accepted December 22, 1999.

ible" [White, 1991], there have been no subsequent chemical analyses to support these assumptions.

This study examined the digestive response of *Varecia variegata* fed diets of varying fiber concentrations.

METHODS

As part of a larger study examining digestive capabilities in non-human primates [Edwards and Ullrey, 1999], five individually housed adult female ruffed lemurs (three red ruffed [*Varecia variegata rubra*] and two black and white ruffed lemurs [*Varecia variegata variegata*]) were included in four separate experiments. All animals were evaluated to be in good health for the duration of the project. Body weights were collected at the onset of the first trial, during the crossover transition period to the second trial diet, and at the completion of the trials. In each experiment, a crossover design was used so that each animal's response was measured for both diets. The experimental protocol was coordinated within the established routines of daily animal care and enclosure maintenance.

Two extruded test diets, each from a single manufactured lot, were offered ad libitum, comprising 100% of the offered diet during the trial period. Fiber concentration was the primary variable of the two test diets. Both diets were formulated to meet or exceed the known 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], hemicellulose [HC]), and gross energy (GE) were measured for the two test diets. Test subjects were gradually transitioned from the standard mixed diet of primate biscuits, fruits and vegetables to the test diet as the sole dietary source. Food intake was measured daily to ensure that ad libitum quantities of the test diet were offered. After a 7-day adaptation period to the offered test diet, 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 passage and digesta retention times (RT) 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 markers were synthesized using methods described by Udén [1978]. The markers were mixed with ground test diet (£20 g) and fruit nectar (£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, hand-fed to each subject, and consumed in their entirety.

Acetate bead markers were offered in quantities of 110 pieces. 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.

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

	Percentage by weight[a]	
Ingredient	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 premixb	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

[a]Air-dry basis

[b]Formulated to provide per kilogram of diet: 8,000 IU vitamin A, 1,750 vitamin D_3, 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 B_{12}, 200 mg choline, 25 mg Fe, 10 mg Cu, 90 mg Zn, 45 mg Mn, 1 mg I, 0.23 mg Se.

[c]MonoProp™ (50% propionic acid on verxite), Anitox Corporation, Bulford, GA.

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 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.

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

	Diet	
Ingredient	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

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The mean retention time, including transit time ($R_{GIT} + TT_1$), was calculated as $R_{GIT} + TT_1 = S(Y_i \bullet t_i) / SY_i$, where Y_i = concentration of markers within the collected sample at t_i and t_i = mean time (hours) after dosing [Blaxter et al., 1956]. TT_1 was determined as the time between dosing and first appearance of the marker in the feces. R_{GIT} was determined by subtracting TT_1 from $R_{GIT} + TT_1$.

Statistical comparisons of response criteria between diets were made by a paired *t*-test.

RESULTS

Animal body weight was lower when maintained on diet 30ADF than when consuming diet 15ADF ($P < 0.01$) (Table 3).

DM intake was expressed as grams of DM consumed per day (24 hours) and as a function of the animal's body weight (g/kg BW or %BW) (Table 3). Statistical differences in DM intake between diets 15ADF and 30ADF were observed. DM intake of diet 30ADF was statistically higher than diet 15ADF when expressed as grams per day ($P < 0.05$) and as a function of body weight ($P < 0.01$).

The apparent DM digestibility (ADMD) of diet 30ADF was statistically ($P < 0.05$) lower than that of diet 15ADF (Table 4). The digestible energy intake of the two test diets as a function of metabolic body size ($kg^{0.75}$) did differ ($P < 0.01$) (Table 4). There were no statistical differences seen between the digestible energy content or digestibility of individual cell wall components (NDF, ADF, C, HC) between diets 15ADF and 30ADF ($P < 0.01$) (Table 5).

There were no statistical differences ($P > 0.01$) 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 were also compared with each other to determine the level of correlation for the parameters measured (TT_1, R_{GIT}). TT_1 and R_{GIT} as estimated by different markers within diets 15ADF and 30ADF were not correlated.

DISCUSSION

Body Weight

The initial mean body weight (4.68 ± 0.30 kg) was higher than the species mean (3.6 ± 0.34 kg) for captive specimens reported by Terranova and Coffman [1997] and was in excess of the weight threshold (4.27 kg) that those authors used to

TABLE 3. Mean body weight (BW) and mean dry matter intake (DMI) of ruffed lemurs (*Varecia variegata* spp) fed diets 15ADF and 30ADF grouped by sub-species and species

				DMI		
Species	Diet	*n*	BW (kg)	g/day	g/kg BW	% BW
Varecia variegata rubra	15ADF	3	4.58±0.33	139.0±43.5	30.0±7.6	3.00 ± 0.76
	30ADF	3	4.00±0.28	183.8±41.0	45.6±7.2	4.56 ± 0.72
Varecia variegata variegata	15ADF	2	4.83±0.25	132.4±9.1	27.5±3.3	2.75 ± 0.33
	30ADF	2	4.10±0.42	280.8±0.0	68.8±7.1	6.89 ± 0.71
Varecia variegata spp	15ADF	5	4.68±0.30[a]	136.3±31.3[a]	29.0±5.8[a]	2.9± 0.58[a]
	30ADF	5	4.04±0.29[b]	222.6±60.5[d]	54.9±14.2[b]	5.49±1.41[b]

[a,b]Values in same column with different superscripts differ ($P < 0.01$).
[c,d]Values in same column with different superscripts differ ($P < 0.05$).

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TABLE 4. Mean apparent dry matter digestibility (DMD), digestible energy (DE) of diets 15ADF and 30ADF, and digestible energy intake (DEI) for ruffed lemurs (*Varecia variegata* spp) grouped by sub-species and species

				DE		
Species	Diet	*n*	DMD	(%)	% kcal/g	kcal/kg.75
Varecia variegata rubra	15ADF	3	53.3 ± 3.0	48.8 ± 5.8	2.18 ± 0.26	96.5 ± 26.95
	30ADF	3	41.2 ± 5.6	39.1 ± 7.4	1.71 ± 0.32	108.4 ± 7.48
Varecia variegata variegata	15ADF	2	47.7 ± 5.6	44.4 ± 1.9	2.25 ± 0.46	90.4 ± 9.07
	30ADF	2	42.5 ± 8.9	40.8 ± 8.7	1.79 ± 0.38	173.6 ± 23.54
Varecia variegata spp	15ADF	5	51.0 ± 4.7[c]	47.0 ± 4.84	2.20 ± 0.29	94.1 ± 19.87[a]
	30ADF	5	41.7 ± 6.0[d]	39.7 ± 6.88	1.74 ± 0.30	134.5 ± 37.95[b]

[a,b]Values in same column with different superscripts differ ($P < 0.01$).
[c,d]Values in same column with different superscripts differ ($P < 0.05$).

define obesity among captive specimens. Although mean body weight was reduced below this obesity threshold after consumption of diet 30ADF (4.04 ± 0.29 kg), it still exceeded the species mean mentioned above.

Digestibility

The relatively low ADMD seen in this study (51.0% of 15ADF and 41.7% of 30ADF) suggests this species lacks specific gastrointestinal adaptations to maximize potential energy substrates (e.g., cellulose), as well as nutrients contained within a fibrous diet. The significant reduction in body weight when consuming diet 30ADF further supports this species reduced ability to utilize a diet with elevated levels of plant cell wall. Although DM intake increased when consuming 30ADF, there was a concurrent reduction in ADMD. As food was available ad libitum, it appears that the animals were unable to extract adequate caloric energy to support body mass when consuming a diet of this fiber concentration.

Despite the comparatively reduced ADMD demonstrated by *Varecia* spp, >20% of the plant cell wall (NDF) and nearly 40% of the HC consumed was degraded by these individuals. Thus, *Varecia* spp do have a limited capacity for fermentative digestion. Similar observations were reported for other frugivorous/omnivorous prosimians [Clemens, 1978].

Although not observed during these studies, ruffed lemurs have demonstrated coprophagic behavior in captivity (personal observation). This behavior allows an animal to re-ingest end-products of microbial fermentation, such as microbial protein, amino acids, and synthesized vitamins lost in the feces owing to limited absorption in the hindgut (cecum or colon) [Oftedal and Allen, 1995]. Such nutrient

TABLE 5. Mean digestibility (%) of various fiber components (NDF, ADF, C, HC) in diets 15ADF and 30ADF by ruffed lemurs (*Varecia variegata* spp) grouped by sub-species and species

Species	Diet	*n*	NDF	ADF	C	HC
Varecia variegata rubra	15ADF	3	22.9 ± 1.1	12.1 ± 4.8	15.2 ±2.0	40.3 ± 1.2
	30ADF	3	19.0 ± 7.4	10.6 ± 7.6	6.6 ± 8.1	38.0 ± 0.7
Varecia variegata variegata	15ADF	2	16.6 ± 1.5	5.3 ± 0.2	5.9 ± 4.0	36.5 ± 1.2
	30ADF	2	23.3 ± 8.5	15.8 ± 11.8	11.9 ± 11.5	40.3 ± 0.7
Varecia variegata spp	15ADF	5	20.4 ± 3.6	9.4 ± 5.0	11.5 ± 5.7	38.8 ± 4.1
	30ADF	5	20.7 ± 7.1	12.6 ± 8.5	8.7 ± 8.6	38.9 ± 5.1

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TABLE 6. Mean transit time (TT_1, hours) of various markers, acetate beads, Co-EDTA, and Cr-mordanted fiber, in diets 15ADF and 30ADF for ruffed lemurs (*Varecia variegata* spp) grouped by sub-species and species

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
Varecia variegata rubra	15ADF	2.5 ± 1.7 (3)[a]	3.5 ± 3.5 (3)	2.5 ± 1.7 (3)
	30ADF	3.5 ± 3.5 (3)	2.5 ± 1.7 (3)	3.5 ± 1.7 (3)
Varecia variegata variegata	15ADF	3.0 ± 2.1 (2)	1.5 ± 0.0 (2)	1.5 ± 0.0 (2)
	30ADF	1.5 ± 0.0 (2)	3.0 ± 2.1 (2)	1.5 ± 0.0 (2)
Varecia variegata spp	15ADF	2.7 ± 1.6 (5)[a]	2.7 ± 2.7 (5)	2.1 ± 1.3 (5)
	30ADF	2.7 ± 2.7 (5)	2.7 ± 1.6 (5)	2.7 ± 1.6 (5)

[a] *n* in parentheses.

recycling may permit the ruffed lemur to recover the undigested nutrients lost in fecal matter.

Digesta Passage and Retention

Results of transit time obtained in this study were comparable with, but slightly longer than, qualitative values reported by Cabre-Vert and Feistner [1995] for *Varecia variegata* fed mixed diets. The differences are mostly likely owing to the variation in experimental method, primarily the frequency of fecal sample collection, and diets offered.

The high rate of digesta passage suggests that limited digestion of insoluble plant material requires an increased turnover of ingesta. With lower GE digestibilities, *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 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.

Implications for Captive Management

Fiber concentrations offered the study subjects in these trials are higher than those traditionally used in captive diets for this species. In fact, the 15ADF test diet is comparable with the highest fiber, commercially available primate diets that are

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 ruffed lemurs (*Varecia variegata* spp) grouped by sub-species and species

Species	Diet	Acetate bead	Co-EDTA	Cr-fiber
Varecia variegata rubra	15ADF	7.5 ± 4.3 (3)a	4.0 ± 2.7 (3)	3.1 ± 2.3 (3)
	30ADF	6.3 ± 1.9 (3)	3.3 ± 0.8 (3)	1.6 ± 0.4 (3)
Varecia variegata variegata	15ADF	2.2 ± 1.6 (2)	4.3 ± 1.7 (2)	5.0 ± 5.4 (2)
	30ADF	2.3 ± 0.3 (2)	1.1 ± 0.1 (2)	3.4 ± 0.4 (2)
Varecia variegata spp	15ADF	5.4 ± 4.2 (5)	4.1 ± 2.1 (5)	3.8 ± 3.3 (5)
	30ADF	4.7 ± 2.6 (5)	2.4 ± 1.4 (5)	2.3 ± 1.0 (5)

[a] *n* in parentheses.

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marketed for specialized folivorous primates such as *Alouatta*, *Colobus*, and *Trachypithecus*. It is clear from this study that, although classified as a "frugivore," *Varecia* spp are capable of utilizing a diet with this level (15% ADF) of fiber. Even though nearly 80% of the plant cell wall is lost in fecal material, one should not overlook the contributions of this indigestible fraction of the diet. Often considered a "negative feed factor," the beneficial role of plant fiber regarding satiety, fecal consistency, and overall gastrointestinal health in primates [Morin et al., 1978; Newberne and Hayes, 1979; Krombach et al., 1984] including humans [Cummings, 1978], has been well documented.

CONCLUSIONS

1. Ruffed lemurs (*Varecia variegata*) are capable of extracting digestible energy from an extruded diet with 15% ADF offered in ad libitum quantities sufficient to maintain body mass.
2. Increased intake of an extruded diet with 30% ADF was not adequate to compensate for reduced DM digestibility, resulting in short-term loss of body mass.
3. The relatively rapid rate of passage and short retention time combined with low ADMD exposing a large mass of food to digestive processes per unit of time and rapidly passing the undigested portion support the frugivorous feeding strategies described for these species.

ACKNOWLEDGMENTS

Special thanks to the staff and keepers of the Zoological Society of San Diego, especially Connie Carson, Dr. Donald Janssen, Karen Killmar, and Michele Stancer, for providing animals and assistance for this project. Test diets were generously donated by Marion Zoological, Inc. (Plymouth, MN). Sharon DeBar and Dr. Pao Ku provided analytical assistance. We are grateful to Dr. Susan Crissey, Dr. Olav Oftedal, and anonymous reviewers whose comments improved versions of this manuscript. Support was provided by Michigan State University.

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