Nutrient Requirements and Interactions

Dietary Fiber Influences Nutrient Utilization, Growth and Dry Matter Intake of Green Iguanas (*Iguana iguana*)[1,2]

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ABSTRACT   Herbivory is an uncommon feeding strategy in lizards. Appropriate diet formulations for captive lizards should be based on performance measures, yet few data are available on the effect of plant fiber on food intake, nutrient utilization and growth of captive herbivorous lizards. This study was conducted to determine the effect of three levels of dietary fiber on dry matter intake, nutrient and energy metabolizability and growth rate of the green iguana (*Iguana iguana*). Twenty-one captive iguanas were fed nutritionally complete diets containing three levels of dietary fiber: 19, 24, and 27% neutral detergent fiber. The iguanas were fed each diet for at least 12 wk, and total excreta were collected for 11.3 ± 4.0 d (means $\pm$ SEM, range of 7 to 25 d). Diets and excreta were analyzed for dry matter, organic matter, gross energy, neutral detergent fiber, acid detergent fiber, and acid detergent lignin. The study was designed as a Latin square crossover. Across all diets, dry matter intake was proportional to body mass[1.0] (BM). Growth rate was greater ($P < 0.05$) when iguanas were fed the low and medium fiber diets (2.2 and 2.4 g/d, respectively) than when fed the high fiber diet (1.4 g/d). However, mean daily dry matter intake of the three diets [7.2 g/(d·kg BM)] was not different. In general, digestibility of fiber fractions and the metabolizability of dietary energy decreased ($P < 0.05$) as the level of dietary fiber increased. These data suggest that a diet containing less than 27% neutral detergent fiber should be fed if rapid growth is to be sustained during intensive captive production of green iguanas.   J. Nutr. 127: 1501–1507, 1997.

KEY WORDS: • *Iguana iguana* • growth rate • digestibility • neutral detergent fiber • energy intake

Herbivory is an unusual feeding strategy in extant lizards, and it occurs primarily in two families. Of about 3750 extant lizard species (Halliday and Adler 1986), the green iguana is one of the most folivorous (Rand 1978). Reptilian herbivores may differ from mammalian herbivores in many respects, although the process of fiber digestion seems similar. Anaerobic microbial species, including cellulolytic species, that ferment plant material have been identified from the hindgut of green iguanas (McBee and McBee 1982). Volatile fatty acids (the usable end-products of anaerobic fermentation) have been identified and production rates measured in digesta samples taken from the hindgut of green iguanas (McBee and McBee 1982, Troyer 1984b). Furthermore, important morphologic adaptations have been identified that are consistent with hindgut fermentation and digesta retention (Iverson 1980 and 1982).

There are compelling reasons to determine the digestive performance and nutrient requirements of a species such as the green iguana. First, the green iguana is an increasingly popular companion animal and an important exhibit species for zoos. Appropriate diets are important for maintaining health, as well as for captive breeding. Second, the green iguana has been an important source of nutrients for some people in Central and South America. People in these regions have hunted and consumed this species for many years. Excessive hunting and habitat destruction have decimated local populations and have prompted the development of new techniques for captive management and farming of this species. Third, the green iguana occupies an unusual folivorous niche in the Neotropics, and its ability to digest plant fiber is intriguing from an ecologic and evolutionary perspective.

The digestibility or indigestibility of some diet constituents has been determined in several species of reptilian herbivores, but inappropriate methodologies, including force-feeding, may have biased these data. The relationship between diet composition and animal performance is a key issue in captive management of green iguanas. Data that are currently available are insufficient to determine the appropriate level of dietary plant fiber for captive herbivorous lizards. One goal of this research project was to determine whether established methods of diet assessment, such as digestion and metabolism trials, could be applied to green iguanas. In addition, the relationships among plant fiber, dry matter intake, nutrient utilization and growth rate in green iguanas are not known. This study was designed

TABLE 1

Ingredient composition of three diets with three levels of dietary fiber fed to green iguanas

Ingredient	Dietary fiber level		
	Low	Medium	High
	g/100 g		
Corn, ground	27.7	16.7	5.7
Soybean meal (48.5% crude protein)	36.5	33.0	29.5
Alfalfa meal, dehydrated (17% crude protein)	10.0	25.0	40.0
Wheat bran	15.0	15.0	15.0
Soybean oil	3.0	3.0	3.0
Meat and bone meal	2.0	2.0	2.0
Molasses, cane	2.0	2.0	2.0
Limestone	2.0	1.5	1.0
Calcium phosphate dibasic	0.8	0.8	0.8
Vitamin premix[1]	0.4	0.4	0.4
NaCl	0.4	0.4	0.4
Mineral premix[2]	0.2	0.2	0.2

[1] Vitamin premix contained the following (units/kg): all-trans retinyl palmitate 2200 mg, cholecalciferol 15 mg, all-rac-α-tocopheryl acetate 48,000 mg, thiamin 1200 mg, riboflavin 2000 mg, pyridoxine 2400 mg, niacin 36,000 mg, pantothenic acid 9600 mg, biotin 100 mg, folate 1600 mg, vitamin B-12 6 mg, choline 600,000 mg.

[2] Mineral premix contained the following (mg/kg): iron 40,000, copper 4000, zinc 40,000, manganese 52,000, iodine 160, selenium 80.

to determine the effect of three different levels of dietary plant fiber on dry matter intake, dry matter, fiber and energy utilization, and growth rate of captive green iguanas fed a manufactured diet.

MATERIALS AND METHODS

Twenty-one green iguanas (*Iguana iguana*), hatched in Panama as part of a captive breeding program, were brought to the Department of Zoological Research, National Zoological Park (Washington, DC) and individually housed for this study. The iguanas were approximately 2.5 y old when the study began in May 1988. The study concluded in April 1989. Protozoa or other flagellate parasites were observed either directly or by flotation techniques in fecal samples, and all animals were treated orally with ivermectin (MSD Agvet, Rahway, NJ) twice prior to the start of the study. Fluorescent lights were on a 12-h light:dark cycle, and an infrared light was suspended approximately 0.5 m over each cage to provide heat. All procedures used in this study were approved by the Animal Welfare Committee of the National Zoological Park.

This study was designed as a Latin square experiment. All iguanas received each of the three dietary fiber levels and the iguanas were blocked into homogeneous groups based on initial body weight (a total of seven blocks). Iguanas were randomly assigned to one of three diet sequences. The iguanas consumed the diets for approximately 12 wk and then were gradually switched to a different diet (over a 7- to 10-d adaptation period).

Diets were in the form of a ground meal that the iguanas readily consumed without the need for force-feeding. Diets were produced in two batches by a commercial supplier (Zeigler Bros. Inc., Gardners, PA) to meet our specifications and were stored in a freezer for the duration of the study. Nutrient intakes of iguanas were calculated based on nutrient composition of each batch to control for small changes in nutrient concentrations between the two batches. The three diets were similar in ingredient and chemical composition except for concentrations of plant fiber (**Tables 1** and **2**). Designations of low, medium and high fiber refer only to the relative amounts of

fiber in these three diets. Plant fiber levels were manipulated by altering the relative amounts of corn, soybean meal and alfalfa meal in the diet. As a consequence of the manipulation of these ingredients, cellulose and lignin concentrations differed among the three diets, but hemicellulose concentration was similar in all three diets (Table 2). Small adjustments were made in the limestone concentration of the diets to maintain comparable calcium:phosphorus ratios.

At the beginning and end of each period, iguanas were weighed on an electronic balance, and cloacal temperatures were measured using an electronic thermometer probe, immediately after the iguanas were removed from their cages. A temperature change associated with agitation due to handling was avoided by measuring temperatures immediately.

Iguanas were offered fresh diet three times per week (Monday, Wednesday and Friday), usually in the morning. Enough diet was offered to ensure that food was always available. Amounts offered were increased as the iguanas grew and their intake increased. Food consumption was determined by weighing the amount of diet offered and reweighing the uneaten portion 24 or 48 h later. Any diet that spilled was collected and reweighed. The amount of diet consumed was determined as the difference between the amount offered and the uneaten amount reweighed. Initial analysis showed that there was little change in diet moisture content associated with ambient conditions. Iguanas had free access to water.

TABLE 2

Nutrient composition of three diets with different levels of dietary fiber fed to iguanas[1]

Nutrient	Dietary fiber level					
	Low		Medium		High	
	g/100 g dry diet					
Crude protein[2]	29.3	± 0.4	28.7	± 0.4	29.1	± 0.3
Crude fat	6.2	± 0.1	6.4	± 0.2	5.8	± 0.2
Crude fiber[2]	5.9	± 0.1	9.3	± 0.5	12.4	± 0.7
Acid detergent fiber (ADF)	11.0	± 0.2	16.0	± 0.3	19.6	± 0.6
Neutral detergent fiber (NDF)	18.6	± 0.6	23.6	± 0.6	27.3	± 0.7
Acid detergent lignin	2.5	± 0.1	4.5	± 0.1	6.5	± 0.8
Cellulose[3]	8.5		11.5		13.1	
Hemicellulose[4]	7.6		7.6		7.6	
Ash	8.5	± 0.1	8.8	± 0.1	9.5	± 0.1
Calcium[2]	2.02		2.06		1.96	
Phosphorus[2]	0.87		0.83		0.82	
Magnesium[2]	0.30		0.31		0.33	
Potassium[2]	1.61		1.80		2.05	
Sodium[2]	0.20		0.22		0.20	
	mg/kg dry diet					
Iron[2]	471		553		615	
Zinc[2]	253		278		267	
Copper[2]	33		35		35	
Manganese[2]	293		327		317	
Molybdenum[2]	2.9		3.9		3.7	
Selenium[2]	0.38		0.41		0.43	
	kJ/kg dry diet					
Gross energy	18.87 ± 0.08		18.91 ± 0.04		18.87 ± 0.13	

[1] Values are means ± SEM, *n* = 2–6 analyses (duplicate analyses for minerals). Air-dried diets contained 92 g dry matter/100 g diet.

[2] Analyzed by New York Dairy Herd Improvement Corporation (Ithaca, NY).

[3] Calculated as difference between ADF and lignin.

[4] Calculated as difference between NDF and ADF.

Metabolism trials were initiated after the iguanas had consumed the diet for approximately 8 wk. To determine the starting and ending points of excreta collection, iguanas were pulse-dosed with 0.15% brilliant blue (FD&C #1, Allied Chemical, Morristown, NJ) in their diet for 1 d. Collections started at the first appearance of the marker in the feces, ended with the first appearance of a second dose of the marker, and lasted 11.3 ± 4.0 d (mean ± SEM, range of 7–25 d). Fecal and urinary excreta were collected together and pooled for an individual iguana over the collection period. The samples were collected into pre-tared containers. During the collection periods, fresh diet was offered on a daily basis. Samples of diet (at least 5 kg) were collected and stored in a freezer for subsequent nutrient and energy analyses.

Excreta samples were freeze-dried and immediately reweighed. The samples were then ground in a mill (Intermediate Model, Thomas-Wiley, Philadelphia, PA) fitted with a 2-mm screen. Subsamples were dried in a forced-air convection oven at 105°C to determine dry matter content of the previously freeze-dried samples. The corrected dry matter was determined as the product of the fractional freeze-dried weight and the weight of the oven-dried subsamples. Diets and excreta were analyzed for ash, neutral detergent fiber, acid detergent fiber, acid detergent lignin and gross energy. Diets also were analyzed for crude protein, crude fat and minerals. Crude protein and minerals were analyzed by a commercial laboratory (New York Dairy Herd Improvement Corp., Ithaca, NY). Crude fat was determined by methylene chloride extraction (FES 80, CEM Corp., Matthews, NC). Ash was determined by combustion at 650°C. Gross energy was determined by adiabatic bomb calorimetry (Parr Instrument, Moline, IL). The residue remaining after combustion of the subsample in the bomb was titrated with 0.0287 mol/L sodium carbonate to correct for the heat of formation of nitric acid and sulfuric acid. Fiber fractions were determined by the methods of Van Soest (Robertson and Van Soest 1981) using a Fibertec system (System M, Tecator AB, Höganäs, Sweden). Heat-stable α-amylase (Sigma Chemical, St. Louis, MO, catalog no. A-3306, 200 μL/sample) and protease (Sigma, catalog no. P-3910, 5 mg/sample) were used to facilitate filtration during fiber analysis. Neutral detergent fiber samples were preincubated with α-amylase for 1 h at 60°C and then incubated with the protease for 1 h at 80°C prior to refluxing with the neutral detergent. Cellulose was calculated as the difference between acid detergent fiber and acid detergent lignin. Hemicellulose was calculated as the difference between neutral detergent fiber and acid detergent fiber. Preliminary studies using urate-spiked excreta samples provided data that indicated urates in the excreta did not interfere with neutral detergent fiber or acid detergent fiber analysis or recovery.

Collected excreta were a combination of fecal and cloacal wastes. The apparent digestibility of fiber fractions could be calculated because there were no quantitatively significant fiber components excreted in non-fecal wastes. However, metabolizability coefficients were calculated for dry matter and energy because the excreta contained a non-fecal source of these components. Metabolizable energy intakes were determined as the difference between gross energy intake and gross energy of the excreta. No correction was made for energy loss of skin by ecdysis. Nutrient intakes were calculated on a daily basis to correct for differences in the length of the collection periods for different iguanas. Furthermore, intakes were calculated on a body mass basis (BM$^{1.0}$) to adjust for differences in body mass among iguanas. The scaling factor BM$^{1.0}$ was used based on regression analysis of log daily dry matter intake and log BM (see Results). Metabolizability and digestibility coefficients were calculated using the direct method (without internal or external markers) because total excreta collections were feasible (Schneider and Flatt 1975). Percent apparent metabolizability or digestibility coefficients were calculated as

$$\frac{\text{Nutrient intake (g or kJ)} - \text{Nutrient excreted (g or kJ)}}{\text{Nutrient intake (g or kJ)}} \times 100.$$

Mean daily mass gain was determined as the difference between final and initial mass, divided by the number of days between measurements.

Data were analyzed with PC-SAS version 6.03 (SAS 1985). The data were first tested for normality and subsequently tested for homogeneity of variance. Variance was analyzed by Spearman correlation analysis of the absolute values of the residuals and predicted values, and by graphic analysis plotting residuals and predicted values. These two assumptions of ANOVA were met (normality and homoscedasticity of variance); therefore, ANOVA was used to determine the effects of diets. The statistical model included square, iguana(square), period(square), and diet. Least-squares means and probability of the difference of the least-squares means were used to contrast diet means. Gross energy of excreta from one animal during one period (medium fiber diet) was not determined (insufficient sample size), so metabolizable energy content and energy metabolizability were not determined for that individual. Statistical significance was determined at the $P < 0.05$ level. Values in the text are means ± SEM.

RESULTS

Cloacal temperature of the iguanas used in this study was 31.8 ± 0.2°C. Although iguanas were randomly assigned to a sequence of diets at the beginning of the study, initial BM of iguanas when fed the low fiber diet was slightly lower ($P = 0.08$) than initial BM of iguanas when fed the medium and high fiber diets (**Table 3**).

Rate of BM gain and feed efficiency were lower when iguanas were fed the high fiber diet than when they were fed the medium or low fiber diet. There was no difference in rate of BM gain and feed efficiency between iguanas when fed the medium and low fiber diets (Table 3).

During the study period, mean BM ranged from 294 to 1602 g. To determine the appropriate scaling factor for BM, $\log_{10}$ mean daily dry matter intake was regressed on $\log_{10}$ mean BM. The slope 1.03 ($r^2 = 0.72$) did not differ from 1.0 (**Fig. 1**). The log-linear relationship between BM and daily dry matter intake allows daily nutrient and energy intakes to be corrected for individual differences in BM.

Nutrient and energy intakes are presented in Table 3. The overall mean daily dry matter intake was 7.14 g/(d·kg BM), and dry matter intake was not different for the three diet treatments. The range in daily dry matter intake was from 1.08 to 15.98 g/(d·kg BM). Likewise, daily organic matter, gross energy and metabolizable energy intakes were not different for iguanas when fed the three diet treatments. Neutral detergent fiber and acid detergent fiber intakes of iguanas were not different when they were fed the medium and high fiber diets, but both intakes were lower when iguanas were fed the low fiber diet. On the other hand, cellulose and hemicellulose intakes did not differ among the three diet periods.

Nutrient and energy metabolizabilities and fiber digestibilities are presented in **Figure 2.** In general, metabolizability of nutrients and energy decreased with increasing concentrations of dietary fiber. Dry matter, organic matter and gross energy metabolizability were highest when iguanas were fed the low fiber diet and lowest when they were fed the high fiber diet. Dry matter metabolizability did not differ when the iguanas consumed the medium and low fiber diets. Neutral detergent and acid detergent fiber digestibilities were not different when iguanas consumed the medium and high fiber diets or when they consumed the low and medium fiber diets. However, neutral detergent fiber and acid detergent fiber digestibilities of the low fiber diet were higher than those of the high fiber diet. Cellulose digestibility was higher when the iguanas were fed the medium fiber diet than when the iguanas consumed the high fiber diet and was higher during consumption of the low fiber diet compared with the high fiber diet. However, cellulose digestibility was not different when iguanas consumed the low and medium fiber diets. Hemicellulose digestibility was not different when iguanas consumed the medium and

TABLE 3

Performance and daily nutrient and energy intake of green iguanas fed three levels of dietary fiber during three periods of at least 12 wk each[1,2]

Variable	Dietary fiber level			SEM	ANOVA (diet effect) P
	Low	Medium	High		
Animal performance					
Initial body mass, g	540.1	606.3	601.4	21.9	0.0776
Final body mass, g	769.8[a]	861.2[b]	750.1[a]	25.0	0.0092
Rate of mass gain, g/d	2.22[b]	2.35[b]	1.42[a]	0.21	0.0072
Feed efficiency, g gain/g feed	0.28[b]	0.25[b]	0.16[a]	1.33	0.0272
Daily intake[3]					
Dry matter, % BM/d	0.70	0.76	0.69	0.06	0.6946
Organic matter, g/(d·kg BM)	6.40	6.90	6.21	0.56	0.6745
Neutral detergent fiber, g/(d·kg BM)	1.31[a]	1.80[b]	1.93[b]	0.14	0.0116
Acid detergent fiber, g/(d·kg BM)	0.86[a]	1.23[b]	1.32[b]	0.10	0.0092
Cellulose, g/(d·kg BM)	0.68	0.87	0.84	0.07	0.1481
Hemicellulose, g/(d·kg BM)	0.46	0.58	0.61	0.06	0.1518
Metabolizable energy, kJ/(d·kg BM)	92.97	96.94	80.04	8.83[4]	0.3951
kJ/g diet DM	13.34[c]	12.55[b]	11.76[a]	0.21[5]	0.0001
Gross energy, kJ/(d·kg BM)	132.46	143.10	129.74	11.69	0.6479

[1] Values are means, $n = 21$.
[2] Within each row, means with different superscripts are different ($P < 0.05$).
[3] BM = body mass and DM = dry matter.
[4] SEM for low and high fiber diets ($n = 21$); SEM for medium fiber diet is ±9.33, $n = 20$ observations.
[5] SEM for low and high fiber diets ($n = 21$); SEM for medium fiber diet is ±0.23, $n = 20$ observations.

high fiber diets but was lower when the iguanas were fed the low fiber diet.

DISCUSSION

Several theoretical models have been suggested to describe and explain the relationship between rate of digesta passage and rate of digestion (especially fermentation) and how these two processes might interact and influence daily intake and animal performance. Several of these models (batch reactors, continuous-flow stirred-tank reactors, plug-flow reactors) have been developed for invertebrates (Penry and Jumars 1987) and have been adapted to mammalian herbivores (Hume 1989). Physical form and particle size of the diet are important factors in determining physiological responses (e.g., food intake, nutrient digestibility, rate of digesta passage) to dietary manipulations. Furthermore, implications of the effect of force-feeding
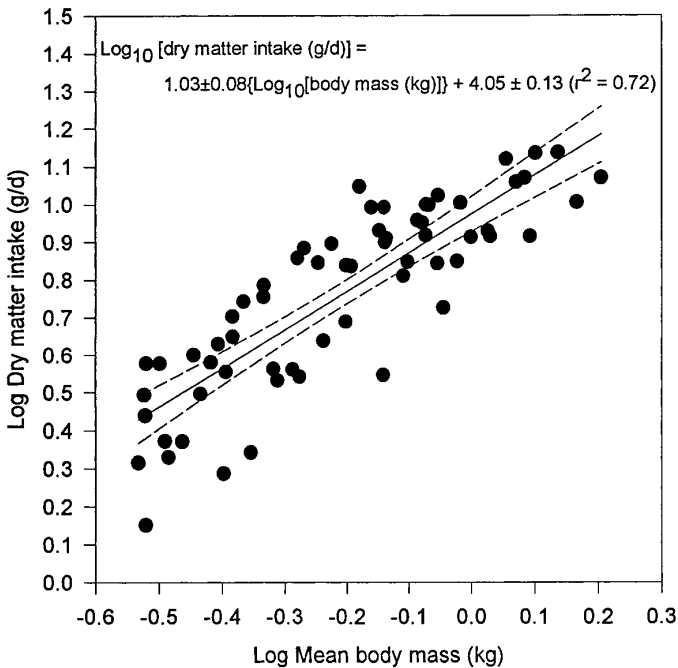

FIGURE 1 Linear relationship (and 95% CI) between $\log_{10}$ body mass and $\log_{10}$ daily dry matter intake of green iguanas.

In the figure:
$$\text{Log}_{10}\,[\text{dry matter intake (g/d)}] = 1.03 \pm 0.08\{\text{Log}_{10}[\text{body mass (kg)}]\} + 4.05 \pm 0.13 \ (r^2 = 0.72)$$
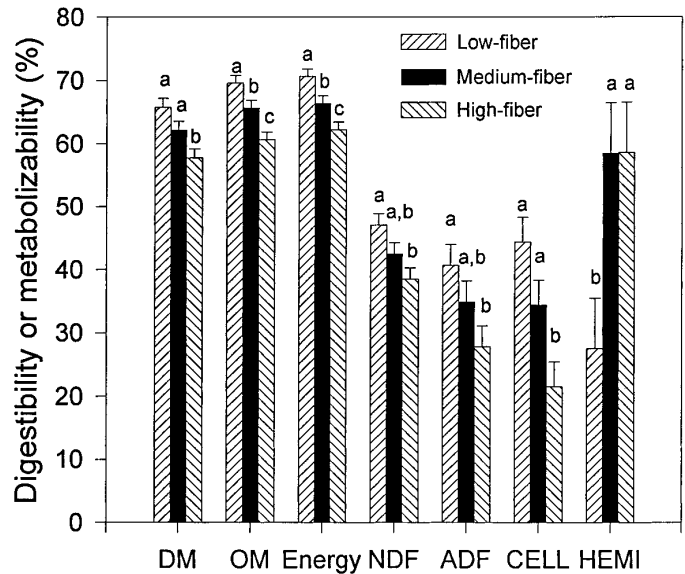

FIGURE 2 Effect of dietary plant fiber content on digestibility of fiber fractions (NDF = neutral detergent fiber, ADF = acid detergent fiber, CELL = cellulose, HEMI = hemicellulose) and metabolizability of dry matter (DM), organic matter (OM) and energy for green iguanas fed three diets during three 12-wk periods. Values are means ± SEM, $n = 21$. Means with different letters are different ($P < 0.03$).

finely ground diets to herbivorous reptiles have been elucidated (Bjorndal et al. 1990). However, the relationships of dietary plant fiber intake to nutrient intake, metabolizability and growth rate have not been studied in reptilian herbivores.

Fiber digestion has been measured in the green iguana as well as in several other herbivorous reptilian species (Meienberger et al. 1993, Troyer 1984a and 1984b, van Marken Lichtenbelt 1992, Zimmerman and Tracy 1989). The digestive tract morphology of green iguanas is well suited to support a symbiotic population of microbes for fiber digestion and to retain digesta for fermentation. All species in the subfamily Iguaninae, except one, possess two types of valves in the colon to facilitate fiber digestion: 1) the circular valve and 2) the semilunar valves (Iverson 1980 and 1982). The numbers and types of valves present are species specific (Iverson 1980). It is thought that the function of these valves is to control digesta retention. Green iguanas can retain digesta in the hindgut for fermentation as assessed by volatile fatty acid production and fiber fraction disappearance (Troyer 1984b). In fact, digesta are retained in the hindgut longer than expected (chi-square test) based on the relative volume and length of the hindgut compared with the foregut and small intestine (Troyer 1984b).

In our study, daily dry matter, organic matter and gross energy intakes were not affected by changes in the concentration of dietary fiber. However, there were differences in the apparent metabolizability of these nutrients. Increased concentrations of dietary fiber decreased metabolizability of these nutrients. These diets were formulated to contain different amounts of neutral detergent fiber and acid detergent fiber, but the ratio of these two fiber fractions was similar in all three diets. The hemicellulose concentration was not different among the three diets, and the difference in cellulose concentration among diets was not as great as that for neutral detergent fiber or acid detergent fiber. Thus there was no difference in cellulose and hemicellulose intakes among the three diet periods. In contrast, neutral detergent fiber and acid detergent fiber intakes were different between the high and low fiber diet periods and the medium and low fiber diet periods, but intakes of these components from the high and medium fiber diets did not differ. The absence of a difference in neutral detergent fiber and acid detergent fiber intake between the medium and high fiber diet periods may be related to a slight decrease in daily dry matter intake from the medium to the high fiber diet period even though this change in daily dry matter intake was not significant. The increase in fiber concentration did not offset the decrease in intake, so daily fiber intakes were not different.

Fiber fraction (neutral detergent fiber, acid detergent fiber, hemicellulose and cellulose) digestibilities were affected by fiber concentration. In general, fiber fraction digestibility increased with a decrease in neutral detergent fiber and acid detergent fiber concentration. However, fiber fraction digestibility, except for cellulose, did not differ between the medium and high fiber diet periods. There was also no difference in fiber fraction digestibility, except for hemicellulose, between the low and medium fiber diet periods. Fiber digestibility of the medium fiber diet was medial to that of the low and high fiber diets. However, the pattern of hemicellulose digestibility was different. Hemicellulose digestibility was not different in the medium and high fiber diets but was much lower in the low fiber diet than in the medium and high fiber diets. The similar hemicellulose digestibilities of the medium and high fiber diets may be related to the similar concentration of hemicellulose in these diets. The difference in hemicellulose digestibility between the low fiber diet and the medium and high fiber diets may be related to analytical errors in determining neutral detergent fiber and acid detergent fiber, especially in feces, because hemicellulose is determined by difference. Small errors in neutral detergent fiber and acid detergent fiber analyses may result in relatively large errors in estimates of hemicellulose content (McAllan and Griffith 1984, Van Soest 1994). Furthermore, the endogenous fecal component may include compounds that are measured as part of the acid detergent fiber fraction, and these compounds may be proportionally greater in the excreta when iguanas are fed the low fiber diet rather than the other diets.

Differences in fiber digestion among the diets, especially the large difference between the low and high fiber diets, may be related to the pattern of feed particle retention in herbivorous lizards. Foley et al. (1987) reported that fine particles were not selectively retained in the hindgut of *Uromastyx aegyptius* (a herbivorous agamid lizard), but the method of determining particulate retention was not described. Thus, all feed particles would have a similar rate of passage with little or no compensation for changes in diet composition. In contrast, fine particles can be selectively retained in the hindgut of many mammalian fermenters (Warner 1981). If there is limited or no selective retention of particles, then fiber fed to iguanas in this study might have been more refractory to microbial attack. Microbial attachment requires time (Akin 1986). If the high fiber diet did not induce increased retention time, fiber digestion would be expected to be reduced when iguanas consumed the high fiber diet, as was observed (Fig. 2). Furthermore, if there had been a change in digesta retention, it is likely that daily dry matter intake would have changed, but no significant change in daily dry matter intake was detected (Table 3).

Another possible explanation for the observed lower digestibility of the fiber in the high fiber diet is related to the lignification index (percentage of lignin in the acid detergent fiber) of the three diets. The lignification indices of the three diets were approximately 23, 28 and 33%, for the low, medium and high fiber diets, respectively (Table 1). The higher lignification index of the high fiber diet would suggest that this diet would have the lowest neutral detergent fiber digestibility; the low fiber diet, with a lower index, would have the highest neutral detergent fiber digestibility. These predictions are supported by the data obtained from green iguanas in this study (Fig. 2).

Although dry matter intake and metabolizable energy (ME) intake were similar when iguanas were fed all diets, energy metabolizability was different for all three diets, and it was lowest when iguanas were fed the high fiber diet. Thus, the ME density (kJ/g dry matter consumed) was different in all three diets. The ME density was lowest when iguanas were fed the high fiber diet and highest when they were fed the low fiber diet. The differences in ME intake and density may actually be greater than reported because of the presumably small losses of energy associated with gas production from fermentation that were not measured in this study. Furthermore, the rate of daily mass gain and the ratio of gain-to-feed intake were lowest when iguanas were fed the high fiber diet. Daily rate of gain and gain-to-feed ratio were not different when iguanas were fed the medium and low fiber diets, but there were differences when iguanas were fed the high fiber diet and the low and medium fiber diets.

The iguanas in this study were fed a meal-type diet that consisted of relatively small particles. There was little change in daily dry matter intake of the iguanas in this study in response to a change in energy density (in this case ME). However, the energy density change might not have been severe

enough to alter daily dry matter intake. The change in ME density was only from 11.46 to 10.00 kJ/g dry matter. This difference is smaller than the ranges that elicited an intake response in mammalian herbivores.

As a consequence of the relatively slow rate of digesta passage and large amount of individual variability (e.g., 1– 8 d for the brilliant blue marker to appear in the feces), it was not possible to quantify the rate of digesta flow of the iguanas in this study. The observation that the brilliant blue was usually excreted as a single bolus on a single day suggested that little mixing or selective retention of the digesta occurred. There was a clear demarcation of the marked feces (e.g., those feces that were blue-green) from other feces, even when unmarked feces were excreted at the same time, and this observation might indicate limited digesta mixing (Foley et al. 1992). However, the observation of little mixing or selective retention in iguanas may be a function of the type of diet fed and does not exclude the possibility that selective retention may occur when a diet is consumed that contains larger or heterogeneous constituents, such as a diet containing fruits, flowers and leaves.

Nutrient and energy digestibilities have been measured previously in herbivorous lizards, including the green iguana. These data are summarized by Zimmerman and Tracy (1989). In many of these studies, the animals were force-fed (Karasov et al. 1986, Ruppert 1980, Troyer 1984b, 1984a and 1987, Zimmerman and Tracy 1989). The level of intake imposed and the stress of force-feeding could have influenced digestibility measurements. In several studies, the lizards were fed only one item, such as sweet potato tubers, dandelion leaves or *Lonchocarpus* leaves (Ruppert 1980, Throckmorton 1973, Troyer 1984b and 1987). In the study reported by Throckmorton (1973), the lizards were fed only sweet potato tubers (which are nutritionally incomplete) for at least 4 mo prior to the start of measurements. Long-term feeding of nutritionally incomplete foods can produce nutritional deficiencies that may alter digestive function and other physiological variables. In other studies, adaptation periods have been as short as 4 d (Ruppert 1980), which may be inappropriate because many lizard species have mean retention times that are as long as 7 d (Zimmerman and Tracy 1989). An insufficient adaptation period might not permit gut microbes to adapt to changing substrates in the digesta, resulting in atypical digestive measurements. The effects of force-feeding, monotypic diets or a short adaptation period result in data that are difficult to interpret.

Unfortunately, dry matter intake in several of the previous studies was not reported. In several instances, investigators (Ruppert 1980, Troyer 1987) force-fed lizards an amount based on the estimated energy expenditure from an equation published by Nagy (1982). Dry matter intake was not reported in other studies in which lizards were given free access to food (Christian et al. 1984, Throckmorton 1973).

The ability of green iguanas in this study to digest fiber was comparable to that of mammalian herbivores, including ruminants (Parra 1978). Of course, the absolute amount of fiber digested on a daily basis was relatively low, and growth rate was slow relative to that of mammals. However, the gain-to-feed ratio of these iguanas was comparable to that of domesticated species used for meat or egg production (NRC 1984, 1985, 1988 and 1994).

This study of green iguanas provides baseline data on dry matter, energy and nutrient intake, growth rate, fiber digestibility, and dry matter and energy metabolizability. This information has important implications for the formulation of diets for intensive rearing programs. When the iguanas were fed the high fiber diet (27% neutral detergent fiber, dry matter basis), growth rate, digestibility and feed efficiency were depressed. However, it is possible that free-ranging green iguanas ingesting natural diets may respond differently to variation in the fiber levels of foods, both because of differences in physical form and because the chemical constituents of fiber may differ.

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