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Digestion in an Ectothermic Herbivore, the Green Iguana (*Iguana iguana*): Effect of Food Composition and Body Temperature

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Abstract

In laboratory experiments, the effect of food composition and body temperature on digestive efficiency was investigated in the lizard Iguana iguana *on Curaçao (Netherlands Antilles). In a series of experiments the animals were kept in cages with a temperature gradient and different foods were offered ad lib. Mean selected daytime body temperatures were 35.0°–36.4°C (mean 24 h* T_b*: 31.8°–33.7°C). Mean apparent dry-matter digestibility (DDM) varied from 30.0% to 84.2%, depending on the kind of food. Mean DDM and digestible energy were significantly inversely related to the cell wall components lignin and cutin, and these components could explain most of the variance in DDM (*r *= 0.88). The amount of digestible protein was significantly correlated with crude protein content in the food. Mean transit time of food through the digestive tract varied from 3.9 (berries) to 8.5 (leaves) d. A second series of experiments, in which body temperatures were varied (*T_b *range: 30.0°–36.1°C), showed that an increase in body temperature induced a significant curvilinear decrease of the transit time from 10 d down to 3 d. Dry-matter digestibility, however, was not affected by a change in body temperature. Maximal fresh-food intake was inversely related at a significant level to the transit time. It is argued that body temperature affects the potential digestive capacity of the green iguana.*

Introduction

The evolution of herbivory depends on a set of interrelated adaptations. Protein and carbohydrates of plant cellular contents are often nearly com-

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pletely available to animals while the structural carbohydrates of the cell wall are available only to those animals that harbor the requisite bacteria and protozoa in their digestive tracts. Thus, some herbivores consume or select plant parts for the sake of the cellular contents, rejecting or passing the main part of the cell-wall portions through the digestive tract. The alternative adaptation is the retention of the fibrous cell wall to extract more available energy from it, as found in foregut (Van Soest 1982) and some hindgut fermenters (Foley, Hume, and Cork 1989). Because the rate of digestion of structural carbohydrates is considerably slower than that of the cellular contents, intake is limited by the need to retain these more slowly digesting residues. In the past reptilian herbivores were thought to belong to the first group (rapid passage coupled with limited utilization of plant cell walls), because it was assumed that they lacked the intestinal specializations necessary for fiber digestion (Szarski 1962; Ostrom 1963; Sokol 1967; Nagy 1977). However, the intestinal tract of some herbivorous turtles and lizards in fact have special morphological adaptations (Tiedemann 1817) for the retention of microbes responsible for degradation of plant-wall material (Bjorndal 1979; Iverson 1980; Troyer 1984*b*).

The green iguana (*Iguana iguana*) is one of the relatively few species of lizards living solely on a diet of vegetation throughout its life (Rand 1978; Iverson 1982; Troyer 1984*b;* White 1985). Green iguanas possess a large, partitioned colon with bacteria (McBee and McBee 1982) and huge populations of commensal nematodes (Leussink 1958; Iverson 1982). Hindgut fermentation may supply up to 30%–40% of the energy budget (McBee and McBee 1982), and the digestibility of cell-wall constituents may be as high as 54% (Troyer 1984*a*), indicating that iguanas are able to digest leaf material approximately as effectively as their endothermal counterparts (Nagy and Milton 1979; Van Soest 1982). The natural diet of the green iguana consists of leaves, flowers, and fruits (Rand 1978; Troyer 1984*a*). Diet composition may shift from one food class to another, depending on the season (van Marken Lichtenbelt 1991). Although some information is available on the dry-matter digestibility in green iguanas feeding on leaf material (Troyer 1984*a*), a comparison between digestibilities of different kinds of food available to the animal has not been made. In this study on the green iguana from Curaçao, Netherlands Antilles, several food classes (leaves, flowers, and berries) were examined with respect to the digestibility of several nutrients and to the transit time of the food through the digestive tract.

In comparison with endotherms, the digestion of food in ectotherms is time-consuming (Parra 1978). While the retention time in many herbivorous mammals of less than 3 kg is 2–18 h (Karasov et al. 1986), the food passage time through the intestinal tract of herbivorous lizards amounts to several days (Harlow, Hillman, and Hoffman 1976; Christian, Tracy, and Porter 1984; Troyer 1984*a;* Karasov et al. 1986). Although the reason for this difference has not yet been clarified, there exist morphological and physiological differences between mammals and reptiles that may play a role with respect to digestibility. Reptiles, compared with most mammals, only minimally reduce food particle size, and large particles are digested at significantly slower rates (Bjorndal, Bolten, and Moore 1990). There are indications that the greater intestinal surface area in mammals is the main basis for a faster absorption of nutrients (Karasov and Diamond 1985), thus making relatively rapid transit time optimal. Besides, body temperature may play a role, because lizards have much more variable body temperatures than do mammals. For example, the uptake of glucose in intestinal sleeves increases with temperature (Karasov, Solberg, and Diamond 1985), as does the breakdown of structural carbohydrates by microbial degradation (Hungate 1966). Thus, the rate of digestion is not only determined by the intestinal morphology but also by body temperature. In this study the influence of temperature on dry-matter digestibility, transit time of food, and potential food intake is examined in green iguanas in which food was offered ad lib.

Material and Methods

Experimental Design

The experiments were carried out on Curaçao at the Carmabi Foundation. Because green iguanas recently captured in the wild refused to accept food in captivity and force-feeding might alter the results of the experiments, animals were used that had been living in captivity for more than a year. Before and between trials the iguanas were kept in outdoor cages (100 cm × 50 cm × 40 cm) and were fed leaves, flowers, and fruit. Commercial or animal food was never offered. Only males were used because some of the experiments took place in the egg-laying period. Gravid females tend to eat less in the reproductive stage because developing eggs can use so much space that there is less room for digesta (W. D. van Marken Lichtenbelt, unpublished data).

To determine the influence of food composition and body temperature on digestive efficiency, two series of digestibility trials were performed. In one series of experiments the animals were maintained on a daily 10L:14D photoperiod, functionally also a 10:14 thermoperiod, reflecting approximately the natural period. Dry-matter digestibility of seven different foods was measured. Leaf material was obtained from mature leaves of wild plant species (*Cordia alba* and *Trichilia trifolia*) and from young leaves of cultivated species (*Amaranthus dubius* and *Ipomoea batatas*). Other trials were carried out with the small yellow flowers of *Acacia tortuosa* (native species), the flowers of the *Hibiscus rosa* (exotic), and the berries of *C. alba* (native species). All foods, except *A. dubius, I. batatas,* and *H. rosa,* were part of the natural diet of the green iguanas on Curaçao. The digestibility of *Bourreria succulenta* berries was determined by analysis of feces that were collected in the wild. Because in some periods of the year the diet consisted of these berries for several weeks and the pits of these fruits were defecated intact, the number of ingested berries could be determined by counting the number of pits in the feces. From this number and the dry-matter content of fresh berries collected in the field the dry-matter intake corresponding to the amount of berries found in the feces could be calculated. Dry-matter intake and dry matter of feces were used to calculate the dry-matter digestibility according to the formula presented below (see calculations). In a second set of trials the influence of body temperature on digestion was studied with leaves of *I. batatas* by manipulating the thermoperiod and the amount of infrared radiation.

To control temperature, cages used for the digestibility trials were placed indoors. The dimensions of the cages were 50 cm × 40 cm × 40 cm, with a shade compartment of 40 cm × 20 cm × 20 cm (fig. 1). Small-mesh wire netting was used on top while the bottom was spanned with wire netting

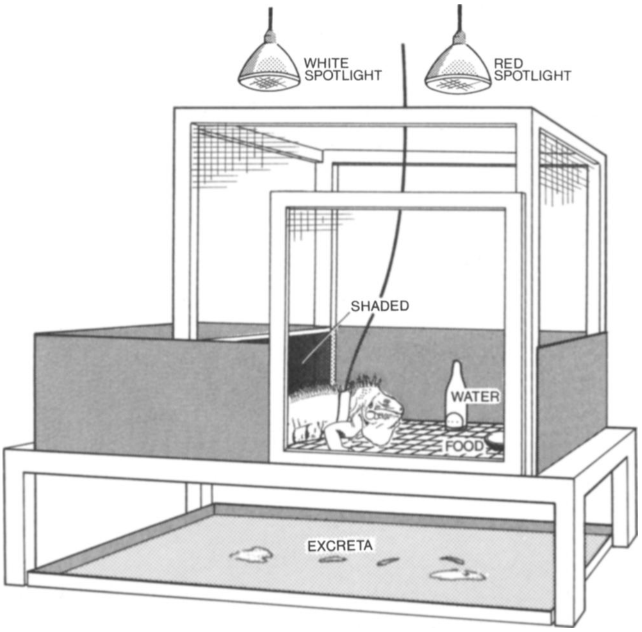

Fig. 1. Cage used for the digestibility trials

with a mesh width of 2 cm allowing the droppings to fall through. The droppings were caught on a plastic tray placed underneath the cage. A 150-W spotlight was fitted 10 cm above the cage. The animals could move freely to and from the shaded and the illuminated part. In one experiment a second 150-W infrared bulb served as an extra heat source and the animals were excluded from the shaded part, ensuring relatively high body temperatures. To test the range of possible body temperatures a copper replica of a green iguana covered with a skin of a green iguana was used (W. D. van Marken Lichtenbelt, J. T. Vogel, and R. A. Wesselingh, unpublished manuscript). The temperature was measured by placing the model directly under the spotlight and in the shaded area. Equilibrium temperature of the model provided a good estimate of the temperature the iguanas could reach (table 1).

Body temperature was measured with a probe mounted on the skin of the chest of the animal. When covered with insulating material (Armaflex) and aluminum foil and fixed into place with leucoplast tape the measured temperature was in good agreement with the deep cloacal temperature ($T_{\text{chest}} = 1.01 \times T_{\text{cloaca}} - 0.35°\text{C}$, $r^2 = 0.995$, $P < 0.001$). In most circumstances the difference between cloaca and chest was less than 0.3°C. During cooling the chest temperature was somewhat lower and during heating of the animal somewhat higher than the cloacal temperature, with a maximal difference of 0.5°C. Temperature was measured by means of a thermistor and an interface connected to an Apple II computer. Body and air temperatures were integrated over 15-min periods, providing a mean temperature for each of these 15-min periods. Body temperature was measured in the temperature experiments with the leaves of *I. batatas* and in the experiments with the berries of *C. alba* and the flowers of *H. rosa*. Temperature was measured for four animals (three with *Hibiscus*).

Each experiment was preceded by a period in which the animals could adapt to the cages. Two strips of plastic surveyors tape (0.5–1 cm long) were fed at the start. Because defecation of complete skeletal networks of leaves is normal in green iguanas, these plastic strips provided acceptable markers for determining the passage rate of the food. The digestibility trial started 3–6 d after the initial markers had passed the digestive tract. Two strips were fed again at the beginning of the trial and in most cases once more after recovery of these strips in the feces. Time elapsed from feeding to the appearance of the markers in the feces provided an estimate of the transit time of the food through the intestinal tract of hindgut fermenters (Van Soest 1982). The experiments lasted, depending on the feeding regime, from 7 d when berries served as food to 19 d with the leaves of *I. batatas* at low body temperatures. During these periods dry-matter intake and total feces production were determined. Fresh food was offered ad lib. from 0900

Table 1

Temperature regimes for the digestibility experiments

Temperature Regime and Food	Spotlight (h)	Red Light (h)	Mount Temperature		Mean Body Temperature	
			Day (°C)	Night (°C)	Day (°C)	Night (°C)
Normal:						
Cordia berry	10	0	29–41	27	35.9 ± .5	29.9 ± .4
Hibiscus flower	10	0	29–41	28	36.4 ± 1.7	31.7 ± 1.6
Ipomoea leaf	10	0	29–41	27	35.0 ± .7	29.6 ± .4
Low:						
Ipomoea leaf	0	0	29–31	27	31.4 ± .0	29.4 ± .1
High:						
Ipomoea leaf	10	24	34–43	32–36	37.7 ± .6	34.6 ± .4

Note. Resulting ranges of possible temperatures are measured with a taxidermic mount. Day and night body temperatures of the experimental animals are means (± SD, $n = 4$, except experiment with *Hibiscus*, in which $n = 3$). At normal temperatures the animals could move freely to and from a shaded and an illuminated part of the cage; at low temperatures there was no extra heat source; at the high-temperature regime the animals had no access to the shaded compartment.

to 1700 hours, with new food being provided at 0900 and 1300 hours. Cloacal excreta were collected twice a day.

Chemical Analyses

Samples of the foods offered, feces, and uric acid (white, often crystalline, material, clearly distinguishable from the feces) were dried at 50°C for preparation for chemical analyses and for determining the water content of the food. The mass of food, feces, and uric acid was determined on an electronic balance accurate to 0.01 g.

For nutrient analyses, dried samples were ground in a Culatti mill with a screen size of 1 mm. Prior to the analyses subsamples were redried at 50°C. All analyses were carried out at least in duplicate. The samples for chemical analyses were weighed on an analytical balance accurate to 0.0001 g. Energy content was determined by an adiabatic bomb calorimeter (Parr) and nitrogen content by the Kjeldahl method. Percentage of crude protein was calculated by multiplying %N by 6.25. The following components were determined according to the methods of Goering and Van Soest (1970), using a Tecator hot extraction unit: NDF (neutral detergent fiber), ADF (acid detergent fiber), lignin (permanganate), cutin, and nitrogen (Kjeldahl) in ADF. Complementary nutrients were calculated as follows: hemicellulose (=NDF − ADF) and cellulose (=ADF − lignin − cutin). Because the crucibles used for the NDF and ADF analyses were often clogged by mucus, a modification of the analytical procedure was carried out. Fifteen minutes before extraction 1 mL *N*-acetyl-L-cysteine (15%) solution was added, causing depolymerization of mucoproteins.

Calculations

The results from the cage experiments were used to calculate digestibilities of several foods as well as digestibilities of the different chemical components and energy.

The following abbreviations and formulas are used: CP, crude protein content in dry matter (%); NDF, neutral detergent fiber content in dry matter (%); ADF, acid detergent fiber content in dry matter (%); DMI, dry-matter intake (g/d); CPI, crude-protein intake (g/d); DDM, apparent digestibility of dry matter (%); DCP, apparent digestibility of crude protein (%); DNDF, apparent digestibility of NDF (%); DEI, digestible energy intake (kJ/d); DE, apparent digestibility of energy (%); MEI, metabolizable energy intake (kJ/d); ME, metabolizable energy as percent gross energy (%); DDM = [(DMI − dry matter of feces)/DMI] × 100; D(nutrient) = [(% nutrient in food × DMI − % nutrient in feces × DM feces)/(% nutrient in food × DMI)] × 100; DEI = [(kJ/g in food × DMI − kJ/g in feces × DM feces)/(kJ/g in food × DMI)] × 100; MEI = DEI − uric acid energy; and ME = [MEI/gross energy intake] × 100.

Because not all the animals used in the cage experiments were in nitrogen balance, the ME was corrected for nitrogen balance (NB) (McDonald, Edwards, and Greenhalgh 1981) by subtracting 30 $\mathrm{kJ} \cdot \mathrm{g}^{-1}$ NB of the above-calculated ME (1 g NB means a deposit of 1 g nitrogen, which is thus not lost as 1 g nitrogen in uric acid [approximately 30 kJ]):

$$\mathrm{MEI(corrected)} = \mathrm{MEI} - \mathrm{NB} \times 30,$$

where NB = N(intake) − N(feces) − N(uric acid). The MEI(corrected) is thus an energy intake value that characterizes the food at NB = 0.

Results

Food Composition and Digestive Efficiency

There were some clear differences in chemical composition between the food classes. Berries, for instance, had high lignin and cutin contents (% DM) and a low protein content (% DM) compared to the other foods (table 2). Flowers had intermediate protein values in comparison to berries and leaves, and NDF values were relatively low. Young leaves had the highest crude protein values. Gross energy content was approximately the same in most foods.

The apparent digestibilities of dry matter (DDM) ranged from 30.0% to 84.2% (table 3). Berries had the lowest digestibility because of a high concentration of cell-wall components, which was caused by the virtually indigestible seeds. Their transit time (3.9 d), however, was the shortest of all studied foods. The seeds of *Cordia alba* contributed 52% of the total dry weight of the berry. Apparently the digestibility of the rest of the fruit amounted to nearly 100%. The digestibility of *Hibiscus rosa* was higher than that of the flowers of *Acacia tortuosa.* This was probably due to the higher lignin and cutin content in *Acacia* flowers. *Acacia* flowers possessed relatively large receptacles that probably contain more structural carbohydrates than the petals. Flowers and leaves cannot be distinguished on the basis of digestibilities only; transit time (TT) through the digestive tract must be considered too. Transit time of flowers was relatively short compared to leaves, although not significantly so (Kruskal-Wallis one-way ANOVA). The (young) leaves of *Ipomoea batatas* at normal temperatures also combined

TABLE 2

Composition of the plant foods used in the digestibility trials

Class and Species	Neutral Detergent Fiber	Cellulose	Hemicellulose	Lignin	Cutin	Crude Protein	Energy Content
Berries:							
Cordia alba	42.2	21.1	1.2	6.5	13.4	11.1	18.4
Flowers:							
Hibiscus rosa	18.7	9.7	5.8	2.4	.9	15.8	17.6
Acacia tortuosa	26.6	3.1	10.9	4.8	7.8	16.4	18.4
Leaves:							
Cordia alba	41.7	2.2	25.5	.9	13.2	21.0	18.6
Trichilia trifolia	35.5	8.6	15.1	5.0	6.8	20.2	18.4
Amaranthus dubius . . .	24.1	5.5	14.7	1.5	2.4	26.5	14.2
Ipomoea batatas	33.5	9.1	18.8	3.2	2.4	31.5	18.7

Note. Data are presented in percentages of dry matter; gross energy content in kJ/g dry matter.

Table 3

Body mass (BW), body-mass changes (ΔBW) and intake and apparent digestibility coefficients of dry matter (DDM), energy (DE), crude protein (DCP), NDF (DNDF), and transit times (TT) of leaves, flowers, and berries and of the leaves of Ipomoea batatas *at different temperature regimes*

Species	BW (g)	ΔBW (%/d)	Intake ($g \cdot kg^{-1} \cdot d$)	DDM (%)	DE (%)	DCP (%)	DNDF (%)	TT (d)
Berries:								
Cordia alba	1,087	−.7	5.52 ± 2.01 (6)	47.0 ± 8.1 (6)	39.9 ± 9.4 (6)	57.7 ± 3.4 (6)	19.8 (2)	3.9 ± 1.7 (6)
Bourreria succulenta				30.0 ± 11.7 (9)				
Flowers:								
Hibiscus rosa	1,168	−.1	5.13 ± 1.01 (3)	84.2 ± .5 (3)	80.0 ± .6 (3)	71.3 ± 1.0 (3)	64.1 ± 3.8 (3)	5.8 ± 2.5 (3)
Acacia tortuosa ...	635	.04	4.23 (1)	53.5 (1)	45.7 (1)	31.4 (1)	10.8 (1)	4.8 (1)
Leaves:								
Cordia alba	817	−.8	2.80 ± .88 (4)	60.1 ± 11.2 (4)	58.5 ± 11.7 (4)	58.7 ± 8.5 (4)	64.0 ± 11.8 (4)	7.0 (2)
Trichilia trifolia ...	838	−.3	1.00 ± .47 (4)	56.3 ± 4.8 (4)	50.1 ± 5.5 (4)	73.4 ± 3.9 (4)	51.7 ± 4.8 (4)	8.5 ± 2.6 (4)

Amaranthus dubius	979	−.3	5.23 ± 2.91 (4)	58.3 ± 5.5 (4)	73.7 ± 3.5 (4)	78.0 ± 7.4 (4)	76.4 ± 4.1 (4)	6.1 ± 2.7 (4)
Ipomoea batatas:								
Low temperature . . .	1,115	−.1	5.12 ± 1.26 (4)	75.3 ± 4.2 (4)	73.7 ± 5.4 (3)	83.1 ± 3.3 (3)	82.2 ± 3.3 (3)	8.4 ± 1.3 (4)
Normal temperature . . .	970	−.3	4.37 ± 1.36 (10)	67.8 ± 8.2 (10)	66.1 ± 6.1 (9)	77.9 ± 2.1 (9)	80.7 ± 3.6 (9)	5.4 ± 1.4 (10)
High temperature . . .	1,022	−.4	5.70 ± 1.37 (6)	70.5 ± 4.8 (6)	67.4 ± 2.6 (3)	81.7 ± 2.3 (3)	78.2 ± 2.0 (3)	4.1 ± 1.1 (6)

Note. Given are the mean values, ± SD, and numbers of animals in parentheses. Body-mass changes (ΔBW) in percentage of initial BW per day. Data from *Bourreria succulenta* are from feces analyses; see text for details.

a high DDM with a low TT, probably because these leaves were crop raised with supplementary fertilizer and water.

It has been recognized in herbivorous mammals (Van Soest 1982) and birds (Nehring and Nerge 1966) that there are inverse relationships between the percentage of cell-wall constituents and DDM. In this study several cell-wall components (lignin, cutin, lignin plus cutin, cellulose, ADF, and NDF) and ratios: percentage lignin/ADF (Troyer 1984*a*) and percentage (lignin + cutin)/ADF were compared with DDM. Dry-matter digestibility was significantly inversely related to most tested cell-wall components concentrations but not to the above-mentioned ratios (table 4). The best predictor for DDM is the percentage lignin plus cutin (fig. 2). A highly significant correlation was found between the ME, corrected for nitrogen balance, and the dry-matter digestibility ($r = 0.91$, $P < 0.001$; fig. 3). Without correction for nitrogen balance the correlation is also significant, but 30% instead of 9% of the variation remains unexplained ($r = 0.70$, $P < 0.001$). The amount of lignin and cutin thus relates to ME.

Digestibility of crude protein can be estimated by CP in dry matter (Robbins 1983). In this study the amount of digestible crude protein was linearly related to the crude-protein concentration in dry matter (fig. 4).

Body Temperature and Digestive Efficiency

The results of the experiments with *I. batatas* at different temperature regimes (low, normal, high) revealed no correlation between body temper-

TABLE 4

Correlations between DDM and cell-wall components (lignin, cutin, lignin + cutin, cellulose, NDF, and ADF)

Component or Ratio	Slope	Intercept	*r*	*P*	*n*
Lignin	−4.81	75.3	.64	.086	8
Cutin	−1.97	72.5	.81	.015	8
Lignin + cutin	−1.81	78.7	.88	.004	8
Cellulose	−1.30	71.2	.58	.133	8
NDF	−1.15	96.1	.74	.036	8
ADF	−.92	78.0	.79	.019	8
Lignin/ADF	27.8	52.2	.14	.75	8
(Lignin + cutin)/ADF	−63.2	88.1	.56	.148	8

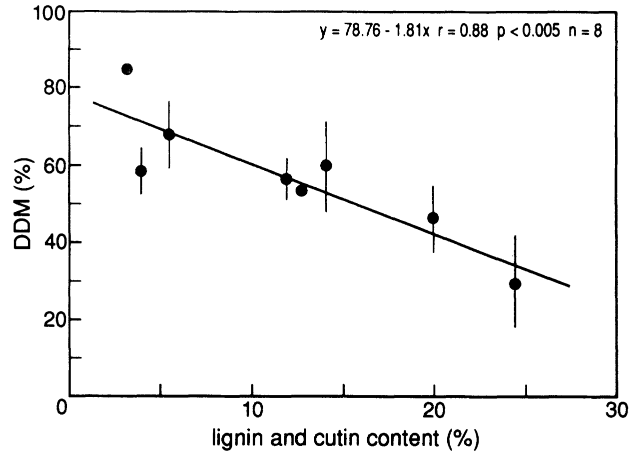

Fig. 2. Relationship between the content of lignin plus cutin and apparent dry-matter digestibility. Data are from table 3 with exclusion of the "high" and "low" temperature experiments.

ature and DDM (fig. 5*A*), and differences between the different temperature regimes were not significant (Kruskal-Wallis one-way ANOVA). Transit time, however, was negatively correlated with body temperature:

$$\mathrm{TT\ (d)} = 459.5 \times 10^{-0.067_b}$$

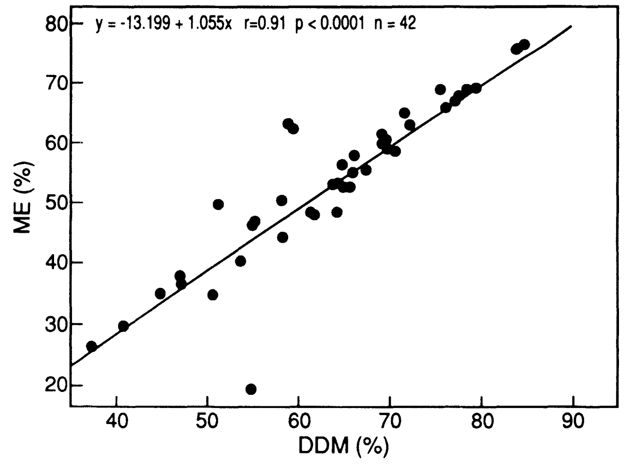

Fig. 3. Relationship between metabolizable energy content (ME) and apparent digestibility of dry matter (DDM), corrected for nitrogen balance. Data are from all experiments of which mean DDMs are presented in table 3.

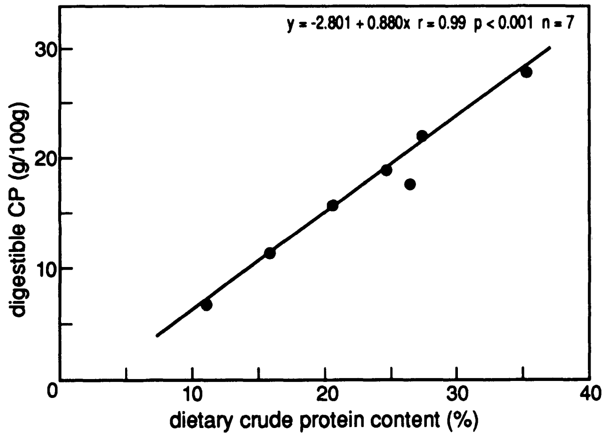

Fig. 4. Relationship between apparent digestible amount of crude protein and crude protein content (CP).

(r = 0.82, $P < 0.05$, n = 12) (fig. 5*B*), and differences between the three temperature regimens were significant ($P < 0.05$, Kruskal-Wallis one-way ANOVA). Intakes at the three temperature regimes did not differ significantly. These results are strengthened by looking at the outcome of the experiments of individual animals, indicated by different symbols in figure 5: all individual iguanas show the same trend of a decreasing TT with increasing body temperature.

Digestive Tract Capacity

The capacity of the green iguana to process food is, among other factors, set by the size of its digestive tract. Stomach capacity determines how much can be eaten in a relatively short time (e.g., one meal). In the colon most of the microbial degradation of the plant material takes place (McBee and McBee 1982). On the short time scale food intake is probably set by stomach capacity and bulkiness of the food. Daily food intake, however, is more complex and is among other things determined by dry-matter digestibility and transit time of the food, the water content of the food, and the rate of water absorption. To obtain an estimate of the digestive tract capacity I examined the relation between TT and food intake. Even though food was offered ad lib., consumption was not always maximal. To avoid contamination of the data by individual points where the consumption was not maximal, the upper 30% of the distribution was selected to fit a regression for stomach capacity, analogous

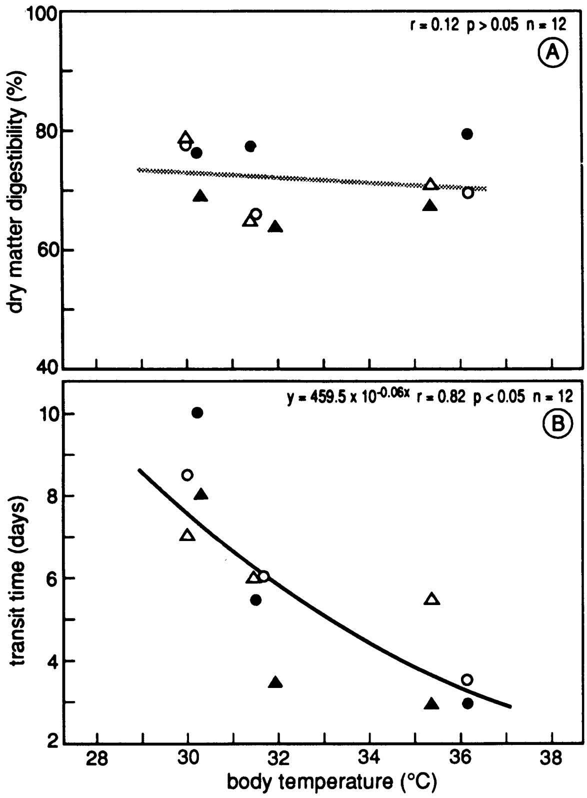

*Fig. 5. Relationship between body temperature and (*A*) apparent digestibility coefficient (DDM) and (*B*) transit time (TT). Data are from temperature experiments with* Ipomoea batatas. *Different symbols refer to different individual animals.*

to the solution chosen by Mautz and Nagy (1987), who accepted the upper 20%. Maximal fresh-food intake was inversely related to transit time of the food (fig. 6):

$$\text{Intake } (\text{g} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}) = 59.4 - 4.01 \times \text{TT}$$

$(r = 0.91, P < 0.001, n = 12)$.

Discussion

Competition between Uptake and Digestion

Ingested food disappears from the digestive tract through two routes, absorption of digested food and passage. Consequently these two processes

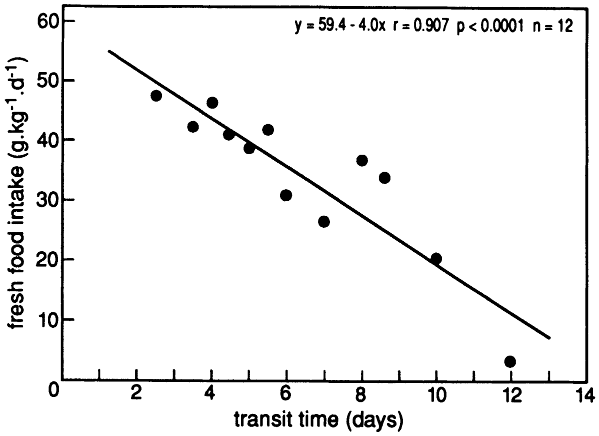

Fig. 6. Relationship between amount of maximum daily fresh food intake and transit time (TT) of the food in the intestinal tract. For selection of data see text.

compete for the same material with some likelihood that potentially digestible or digested matter will be passed to the feces. Passage is necessarily linked to intake because the consumption of more food will enhance the flow of material in the digestive tract. Because food was offered ad lib. the animal determined the degree of fill of the digestive tract. This is why I believe it is better to use animals that are adapted to cage circumstances that have been fed with the appropriate food for a long time rather than to force-feed animals. Moreover, the procedure I followed minimizes any influence of stress. On the other hand it is important that the intake rates are comparable to the intake rates under natural circumstances. Mean daily intakes during the trials were comparable to daily food intake observed in the field (van Marken Lichtenbelt 1991). Comparison of digestive efficiency with data from other studies is difficult not only because of variable temperatures and diets but also because other digestibility experiments carried out with herbivore lizards used force-feeding. The ration used in force-feeding experiments influences transit time and dry-matter digestibility to unknown extents.

Food Composition and Digestion

At "normal" temperatures apparent dry-matter digestibilities of the different food types varied considerably (DDM: 30%–84%). This range is comparable to the range of digestibilities found in other studies on herbivorous lizards (DDM: 36%–86%, table 5) and tortoises (36%–71%, Bjorndal 1989). Diets high in cell contents (*Hibiscus rosa, Ipomoea batatas*) or low in cell-wall digestibility (berries *Cordia alba,* flowers *Acacia tortuosa*), which are digested primarily enzymatically, have slow TTs. Diets with high cell-wall digestibilities requiring relatively slow microbial fermentation (leaves of *C. alba, Trichilia trifolia, Amaranthus dubius*) have short TTs. Bjorndal (1989) reported the same trend in two tortoise species (*Geochelone carbonaria* and *Geochelone denticulata*) in a study comparing digestive processing of fruit and foliage diets.

The range of DDM of leaves in the green iguanas on Curaçao was relatively small (56%–68% at normal temperature). The mean values for leaf DDM measured in force-fed green iguanas in Panama are somewhat lower (50%–53%) (Troyer 1984*a*). However, the TT found in Panamanian green iguanas is generally shorter. The highest digestibilities found in the green iguanas on Curaçao are those of the hibiscus flowers (DDM: 84%; DE: 80%). Throckmorton (1973) also found high energy digestibilities (DE: 86%) of tubers of *I. batatas* in *Ctenosaurus pectinata.* Both hibiscus flowers and tubers have a very low cell-wall content (NDF, lignin, and cutin). Berries, on the other hand, possess a virtually indigestible seed. Digestibility of berries is the lowest of all foods investigated. However low, the DDM could be compensated for by a short TT, presumably because of the high concentration of sugars in the pulp material. Most of the variation in DDM between the different foods studied can be explained by differences in cell-wall components. The best predictor for dry-matter digestibility appeared to be lignin plus cutin concentration in the food ($r = 0.88$); lignin and cutin are virtually indigestible nutrients and limit the use of cell-wall components (Van Soest 1982).

The digestibility of crude protein by the iguanas was positively related to CP and was of the same magnitude as observed for wild ruminants (Robbins 1983). In the green iguana the digestible crude protein amount was linearly related to CP in the food (amount $\text{DCP} = 0.88\text{CP} - 2.80$). This means that in field studies the CP can be used as a predictor for the DCP per food item, although differences in the amount of tannins and other soluble phenolics can reduce the apparent digestibility of protein (Robbins 1983).

The digestibility of NDF was in some cases (i.e., leaves of *I. batatas, C. alba, A. dubius*) high compared with DDM. This is probably caused by the fact that DDM is less than true digestibility (because of gut secretions, microflora, etc.) while DNDF is close or equal to true digestibility of NDF (Van Soest 1982). Hansen and Sylber (in Christian et al. 1984) report high cell-wall digestibilities in *Sauromalus obesus* as well (cellulose digestive coefficient: 82%).

Table 5

Digestive efficiency of dry matter (DDM), NDF (DNDF) and energy (DE), metabolizable energy (ME), transit time (TT), and body temperatures (T_b*) in herbivorous lizards*

							T_b[b]				
Species	Age[a]	BM (g)	DDM (%)	DNDF (%)	DE [ME] (%)	TT (d)	Day (°C)	Night (°C)	Feeding[c]	Food	Reference[d]
Conolophus subcristatus	A	5,340	. . .	39 (cel)	48	6.5	. . .	. . .	ad lib.	*Opuntia* pads	1
Iguana iguana	A	1,304	53	46	. . .	5.5	36 (12)	31	FF	*Lonchocarpus* leaves	2
	A	1,115	75	82.2	74	8.4	31 (10)	29	ad lib.	*Ipomoea batatas* leaves	3
	A	970	68	80.7	66	5.4	35 (10)	30	ad lib.	*Ipomoea batatas* leaves	3
	A	1,022	71	78.2	67	4.1	38 (10)	35	ad lib.	*Ipomoea batatas* leaves	3
	A	817	60	64	59	7	35 (10)	30	ad lib.	*Cordia alba* leaves	3
	A	838	56	52	50	8.5	35 (10)	30	ad lib.	*Trichilia trifolia* leaves	3
	A	979	58	76	74	6.1	35 (10)	30	ad lib.	*Amaranthus dubius* leaves	3
	A	1,087	47	20	40	3.9	35 (10)	30	ad lib.	*Cordia alba* berries	3

	A	1,168	84	64	80	5.8	35 (10)	30	ad lib.	*Hibiscus rosa* flowers	3
	A	635	54	11	46	4.8	35 (10)	30	ad lib.	*Acacia tortuosa* flowers	3
	A	. . .	30	. . .	. . .	. . .	. . .	. . .	Field*	*Cordia alba* berries	3
	J	267	50	57	. . .	3.6	36 (12)	31	FF	*Lonchocarpus* leaves	2
	J	. . .	. . .	. . .	49	3.3	34 (4)	28	FF	*Lonchocarpus* leaves	4
	J	. . .	. . .	. . .	56	3.1	37 (8)	28	FF	*Lonchocarpus* leaves	4
	J	132	73	. . .	. . .	3.8	. . .	. . .	ad lib.	*Ipomoea batatas* leaves	3
Amblyrhynchus cristatus	A	± 1,200	70	. . .	79	. . .	. . .	. . .	Field**	Alga	5
Ctenosaurus pectinata	A	750–1,000	. . .	. . .	86	3.0–5	37 (12)	27	ad lib.	*Ipomoea batatas* tubers	6
Cyclura carinata	A	± 600	. . .	. . .	. . .	3.5–10.5	. . .	. . .	Field	. . .	7
Egernia cunninghami	A	200–300	. . .	. . .	75	. . .	. . .	. . .	. . .	*Trifolium* sp. leaves	8
Sauromalus obesus	A	. . .	47	. . .	. . .	3.1	37–40 (10)	25	FF	Rabbit food	9
	A	. . .	. . .	82 (cel)	. . .	. . .	. . .	. . .	. . .	Flowers, carrots, chick food	10

Table 5 (*Continued*)

Species	Age[a]	BM (g)	DDM (%)	DNDF (%)	DE [ME] (%)	TT (d)	T_b[b]		Feeding[c]	Food	Reference[d]
							Day (°C)	Night (°C)			
	A	...	56	...	50	...	...	...	Field***	Leaves, flowers, fruits	11
	A	206	...	...	65	...	37	20	FF	Flowers, dandelions	12
	A	144	...	...	67	...	37	37	FF	Flowers, dandelions	12
	A	...	67	50	...	3.5, 4.7	36	...	FF (100%)	Rabbit food	13
	A	...	65	51	...	5, 5.5	36	...	FF (50%)	Rabbit food	13
	A	...	65	49	...	5, 5.5	32	...	FF (100%)	Rabbit food	13
	A	...	58	46	...	...	32	...	FF (50%)	Rabbit food	13
	A	...	70	...	...	...	28	...	FF (100%)	Rabbit food	13
	...	...	86	...	83	...	...	...	...	Carrot, dandelion	14
Dipsosaurus dorsalis	A	...	53	...	54	...	33	33	FF	Rabbit food	15
	A	...	60	...	63	...	37	37	FF	Rabbit food	15
	A	...	66	...	69	...	41	41	FF	Rabbit food	15
	A	...	56	...	...	...	41 (12)	28	FF	Rabbit food	15
	A	...	45	...	...	3.2	37–40 (10)	25	FF	Rabbit food	16

	A	49	36	. . .	[29]	5.8	. . .	28 (12)	FF	Natural vegetation (autumn)	17
	A	61	61	. . .	[53]	3	. . .	28 (12)	FF	Natural vegetation (spring)	17
	A	. . .	61	37	61	. . .	41	. . .	FF (100%)	Rabbit food	14
	A	. . .	63	40	61	. . .	37	. . .	FF (100%)	Rabbit food	14
	A	. . .	60	36	57	. . .	33	. . .	FF (100%)	Rabbit food	14
	H	4.2	55	. . .	[54]	3	. . .	28 (12)	FF	Natural vegetation (autumn)	17
	H	7.8	67	. . .	[61]	2.7	. . .	28 (12)	FF	Natural vegetation (spring)	17
Klauberina riversiana	A	14.7	. . .	. . .	89	3.6	30–31 (14)	20–21	ad lib.	*Pyrus malus* fruit (apple)	18

Note. Ellipses indicate data are not available; cel, cellulose.

[a] A = adult; J = juvenile.

[b] In case of cyclic temperature regime, number in parentheses indicates time in hours for temperature.

[c] FF = force feeding; number in parentheses is percentage of estimated maintenance level; *feces analyses; **ADC (DDM) estimated with marker (Mn); ***ADC estimated with doubly labeled water method.

[d] References are as follows: (1) Christian et al. 1984; (2) Troyer 1984*a;* (3) this study; (4) Troyer 1987; (5) Nagy and Schoemaker 1984; (6) Throckmorton 1973; (7) Auth in Auffenberg 1982; (8) Shine 1971 in Johnson and Lillywhite 1979; (9) Karasov et al. 1986; (10) Hansen and Silber in Christian et al. 1984; (11) Nagy and Schoemaker 1975; (12) Ruppert 1980; (13) Zimmerman and Tracy 1989; (14) Voorhees 1981 in Zimmerman and Tracy 1989; (15) Harlow et al. 1976; (16) Karasov et al. 1986; (17) Mautz and Nagy 1987; (18) Johnson and Lillywhite 1979.

Effect of Body Temperature on Digestibility and Rate of Digestion

In this study, body temperature greatly affected the transit time in the green iguana but did not have much influence on the digestibility coefficient (coefficients of variation: 37% in TT vs. 5% in DDM). The digestibility coefficients were not significantly different at the three temperature regimes and were, in view of the long transit times, possibly near their potential maximum. Although food was offered ad lib. no significant difference in intake was observed during the temperature experiments. In contrast with these findings Troyer (1987) showed in juvenile green iguanas in Panama, fed leaves of *Lonchocarpus pentaphyllus* with high contents of cell-wall material, that the digestive coefficient did differ significantly at different temperatures (table 5), although differences in transit time were not significant. Harlow et al. (1976) also reported that body temperature was significantly correlated with apparent digestibility in the desert iguana (*Dipsosaurus dorsalis*). In both studies the animals were force-fed, which, in case of relatively high food levels at moderate temperatures, could explain the different results. The problem of overfeeding has also been discussed by Zimmerman and Tracy (1989). In their experiments with the desert iguana they force-fed the animals at a maintenance level, as calculated on the basis of body temperature. Their results are in agreement with the results of the Curaçao green iguanas. Dry-matter digestibility was not significantly related to body temperature. However, TT of the food in *D. dorsalis* in their study is not known. In another herbivorous iguanine (*S. obesus*), also fed to maintenance, Zimmerman and Tracy (1989) determined that the TT of the food was significantly longer at lower body temperatures. Because these lizards were force-fed less food at lower body temperature regimes, they could not report whether the rate of passage was lower at lower body temperatures because of a direct thermal effect on the physiology of digestion or because of a reduction in bulk flow of digesta. In the green iguana on Curaçao, the animals on average consumed equal amounts of food during the different temperature experiments, indicating that the observed reduction in TT is indeed a direct thermal effect and goes hand-in-hand with a difference in degree of fill of the digestive tract. How transit time is optimized, in view of the time constants of microbial digestion and the rate of absorption of nutrients through the intestinal wall, are matters for further study.

Our study reveals that TT is inversely related to body temperature although dry-matter digestibilities remain comparable, while Zimmerman and Tracy (1989) showed that a decrease in transit time brought about by means of force-feeding results in lower DDM. These facts must have implications for potential food intake. Indeed, our results show that the maximal fresh food intake is inversely related to TT (fig. 6). It will be noted from figure 5 that the dependence of TT on body temperature is a steep one, and it appears a reasonable assumption to interpret the active attainment of high body temperature (35°-36°C) that in this species typically follows active foraging (van Marken Lichtenbelt 1991) as functionally aiming at shortening TT and hence clearing the gut for a further onslaught.

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