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Cellulose Digestion and Nutrient Assimilation in *Sauromalus obesus*, a Plant-Eating Lizard

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Cellulase activity in the large intestine of chuckwallas was similar to that in a cow's rumen. However, tracer evidence that ash-free dry matter assimilation in the large intestine was small indicates that cellulose digestion is not of major importance in the energy balance of these lizards. Gut pH changes and fractional assimilations of K, Na, Cl, Ca, Mg, Fe, Al, Mg, Sr, B and Cu were similar to those in non-ruminant mammalian herbivores.

MORE than 40 of the approximately 2,500 living species of lizards are primarily herbivorous (Pough, 1973). Recent efforts to explain this phenomenon include considerations of 1) the physical strength and structural machinery necessary to bite off and chew up plant material (Szarski, 1962; Ostrom, 1963), 2) modifications of gut morphology and microbial populations required to digest plants (Sokol, 1967) and 3) relationships among body size, energy requirement, energy availability and diet (Pough, 1973; Wilson and Lee, 1974). Knowledge of whether or not herbivorous lizards can digest and assimilate cellulose would seem to be quite important in this regard, but neither the presence of cellulolytic enzymes nor the assimilation of cellulose has been quantitatively investigated in any plant-eating lizard. In fact, very little is known about even the general nature of digestion in reptiles as a group (Skoczylas, 1970a,b; Dandrifosse, 1974).

Cellulases have been found in the digestive tracts of many herbivorous animals, including mammals (Barnard, 1973), birds (McBee, 1971; Ziswiler and Farner, 1972), a tortoise (Smith, 1965) and several invertebrates (Yokoe and Yasumasu, 1964; Elyakova, 1972), and cellulose digestion has been demonstrated in three plant-

eating birds (Inman, 1973). However, neither the presence of cellulolytic enzymes nor the breakdown of cellulose necessarily indicate that cellulose constitutes a significant source of energy for the animal (McBee, 1971).

In this study, cellulose digestion in an herbivorous lizard was examined first by determining the presence and activity of cellulolytic enzymes in various parts of the gut, and then by assessing the progressive changes in the mass of organic material through the digestive tract (tracer method), in order to estimate assimilation of cellulose breakdown products. In addition, the pH in various gut segments was measured, and net assimilations of various nutrients such as nitrogen, electrolytes and several trace elements were determined. These results permit an evaluation of the general nature of digestive physiology in these animals. The lizards used were chuckwallas (*Sauromalus obesus*), which live in the deserts of western North America and are strict vegetarians (Nagy, 1973).

Materials and Methods

Cellulase activity.—To measure gut cellulase, a chuckwalla was captured in May, in Rock Valley, Nye Co., Nevada, and kept cold to inhibit digestive processes until it was killed the next day. Contents of the stomach and small and large intestines were removed and weighed. All of the chuckwallas used in this study had masses of nematode worms in their large intestines, but worms were not seen elsewhere in the digestive tract. Some of the worms were isolated, washed several times in 0.02 M sodium phosphate buffer (pH 6.1), drained and weighed. The tissues comprising each gut segment were also washed and weighed. All samples were then homogenized in cold 0.02 M sodium phosphate buffer and centrifuged at 2000 *g* for 10 min. Some cellulases are normally bound to plant material and are not extracted by dilute buffers, but can be solubilized in concentrated salt buffer (Lewis and Varner, 1970). Accordingly, some samples were also extracted with 1 M NaCl in 0.02 M sodium phosphate buffer.

Cellulase activity in the supernatant solution was assayed using the method of Almin et al. (1967) as modified by Lewis and Varner (1970). This method involves determination of the progressive decrease in the viscosity of a mixture of 0.40 ml carboxymethyl-cellulose solution (1.33 w/v in 0.02 M sodium phosphate buffer) and 0.20 ml enzyme extract by measuring the drainage time through a calibrated section of a 0.10 ml pipette. Viscosity measurements were made each half hr for two hrs, and samples with low activity were measured after nine, 24 and 48 hrs. The reactions and measurements were done at about 23 C. Even though a buffer solution was used, the pH values of the enzyme extracts were near those occurring in the animal (stomach content extract, pH = 2.2; small intestine content extract, 7.8; large intestine content extract, 7.6; gut tissue extracts, 6.5 to 7.7). Thus, the pH of the reaction mixture should not have inhibited any cellulases that were normally active at the pH values existing in the lizard. Results were converted to relative units/g fresh mass of sample per hour according to Almin et al. (1967).

To provide comparable results for interpretive purposes, samples of the contents of the rumen and reticulum of a dairy cow (*Bos tarus*) were assayed for cellulase activity as above. The donor cow had died of unknown causes sometime during the 12 hrs preceding sample collection, but the California State meat inspector present at the autopsy indicated that the stomach contents appeared normal and reasonably fresh.

Composition of diet and gut contents.—Eight chuckwallas were collected in May, near Barstow in the Mojave Desert, California, and were killed within 4 hrs of capture. All of the material in the following gut segments was removed separately: stomach, small intestine, large intestine (including the cecum) and rectum (the posterior part of the large intestine, containing well-formed fecal pellets). Contents of the cloaca were not collected. Gut contents were placed in inert plastic vials, weighed and dried to constant mass at 70 C to determine water content. Dried samples were powdered in a non-metallic container using a Spex Mixer-Mill.

To assess the composition of the food eaten by these lizards, the stomach contents were identified to species before drying, and an average diet was calculated on a dry mass basis (Nagy, 1973). Samples of each plant species eaten were collected in the field and prepared as above, and mean food composition was calculated from individual plant species composition and their dry mass fractions in the average diet.

Nitrogen contents were measured by Kjeldahl digestion, with final ammonia concentration being measured with an Orion ammonia electrode. An Applied Research Laboratories optical emission spectrometer was used to analyze dry samples for calcium, magnesium, iron, aluminum, manganese, strontium, boron and

TABLE 1. CELLULASE ACTIVITY, IN RELATIVE UNITS/g FRESH MASS PER HOUR, IN THE GUT TISSUE AND GUT CONTENTS OF A CHUCKWALLA, AND THE STOMACH CONTENTS OF A COW. Values are means ± S.E. with the number of determinations shown in parentheses.

	stomach	sm. intest.	lg. intest.	nematodes
Chuckwalla:				
tissue	0 (4)	0 (4)	5.9 ± 0.8 (9)	
contents	0 (4)	0 (4)	99.8 ± 4.6 (6) 101.5 ± 7.6[a] (5)	29.8 ± 7.5 (5)
	rumen			
Cow:				
contents	50.7 ± 4.2 (13) 157.2 ± 10.9[a] (6)			

[a] 1 M NaCl extraction—see text.

copper. To determine potassium, sodium and chloride, 1.0 ml distilled water was added to 0.10 g dry, powdered sample and left to soak overnight. Potassium and sodium concentrations in the supernatant fluid were measured with a Coleman flame spectrophotometer, and chloride concentration was determined with a Buchler-Cotlove chloridometer. Unfortunately, the pH of the gut contents was not measured before the samples were dried. However, this was estimated later by determining the pH of rehydrated samples with narrow-range pH indicator paper. Ash contents were determined by combusting samples at 500 C for 5 hrs in a muffle furnace.

RESULTS

There was no detectable cellulolytic activity in chuckwalla stomach or small intestine (Table 1). However, in the large intestine, cellulase activity was about as high as in a cow's rumen. Additional cellulase could be solubilized in 1 M NaCl extracts of rumen contents, but not lizard gut contents. Nematode worms from chuckwalla large intestine contained about 30% of the activity found in their environment.

The composition of the food and the material in the four gut segments is shown in Table 2. In order to examine the progressive changes in the composition of a parcel of food as it is acted upon by digestive and assimilative processes, it is necessary to adjust the mass-specific values in Table 2 to account for changes in the denominator due to assimilation in various gut segments. If some dietary substance (s) is not assimilated, then changes in its mass-specific concentration can be used to calculate changes in the dry matter in any part of the gut with the equation: g unassimilated dry matter remaining = (amount of s/g dry food) ÷ (amount of s/g dry gut material). Previous studies (Nagy and Shoemaker, 1975) indicated that chuckwallas eating a similar diet voided 0.37 g dry feces per g dry food ingested. The only dietary substance measured in this study yielding a similar value (0.31), when food and rectum content measurements were used in the above equation, was manganese. In wild cotton rats (*Sigmodon hispidus*), manganese provided a relatively accurate indicator of dry matter assimilation (Kaufman et al., 1976). Although nutrient assimilation will be slightly overestimated, manganese contents were used to calculate dry matter changes in each gut segment (top line in Table 3), and these values were then used to correct all other values for dry matter assimilation. An estimate of organic matter assimilation was obtained by correcting the dry matter values for ash content (Table 3).

The behavior of dietary substances in the gut can be grouped into three categories, based primarily on whether the amount of the substance in the stomach contents was higher, the same, or lower than in the food. Substances represent-

TABLE 2. COMPOSITION OF THE DIET AND THE MATERIAL IN VARIOUS PARTS OF THE DIGESTIVE TRACT OF CHUCKWALLAS CAPTURED IN MAY. Units other than pH are on a per gram dry mass basis, and means are shown with standard error in parentheses.

	Food[b]	Stomach (N = 7)	Small Intestine (N = 5)	Large Intestine (N = 8)	Rectum (N = 5)
Water, ml	2.53	5.59	8.82	3.81	1.89
	(0.29)	(0.25)	(0.94)	(0.92)	(0.20)
pH[a]	—	2.4	8.6	6.8	6.9
		(0.1)	(0.2)	(0.1)	(0.1)
Ash, mg	218.6	247.2	515.4	623.2	671.6
	(45.0)	(50.4)	(67.4)	(97.1)	(154.2)
Nitrogen, mg	23.1	23.7	8.8	18.4	16.3
	(2.0)	(1.3)	(1.7)	(3.2)	(4.3)
Potassium, mg	24.7	8.48	2.61	4.16	7.69
	(6.2)	(1.32)	(0.34)	(0.66)	(1.83)
Sodium, mg	1.16	3.94	32.58	5.45	0.67
	(0.29)	(0.63)	(3.72)	(0.69)	(0.13)
Chloride, mg	6.56	30.28	11.83	2.66	3.20
	(2.32)	(3.63)	(1.90)	(0.67)	(1.51)
Calcium, mg	27.8	13.0	18.5	33.5	28.9
	(6.7)	(3.6)	(6.9)	(3.3)	(3.8)
Magnesium, mg	4.78	3.33	5.02	7.16	8.05
	(0.94)	(0.57)	(1.25)	(0.53)	(1.32)
Iron, mg	0.67	1.34	1.58	1.79	1.80
	(0.26)	(0.09)	(0.29)	(0.16)	(0.24)
Aluminum, mg	1.01	2.81	2.89	3.61	3.57
	(0.40)	(0.18)	(0.33)	(0.24)	(0.49)
Manganese, μg	77.8	77.8	126.4	260.8	253.5
	(17.1)	(9.9)	(20.0)	(10.0)	(17.6)
Strontium, μg	204.3	126.5	183.4	269.0	239.9
	(44.5)	(14.6)	(47.3)	(22.0)	(37.2)
Boron, μg	88.1	68.4	97.0	105.6	96.5
	(20.2)	(15.2)	(6.0)	(9.3)	(19.1)
Copper, μg	7.3	8.1	8.0	16.3	12.0
	(0.7)	(0.9)	(1.4)	(1.4)	(1.8)

[a] pH of rehydrated dry matter.
[b] Weighted means.

ing each category are plotted in Fig. 1 as percent of the amount in one g dry food that remains in each successive gut segment. Both iron and aluminum showed large increases in the stomach. It is unlikely that the stomach walls were secreting iron and aluminum into the lumen. The probable explanation for this observation is that chuckwallas ate plant material that contained more dust and sand than did the samples of food plants that were collected by hand. Most soils contain high levels of iron and aluminum (Shacklette et al., 1971). The apparent assimilation of both aluminum and iron by the intestines is of interest, because relatively large amounts (ca. 1 mg/dry food ingested) are involved. Ash-free dry matter, nitrogen and possibly copper are in the category of substances that do not appear to be assimilated in the stomach, but in the intestines instead. Those elements that the stomach does absorb include potassium, calcium, magnesium, strontium and boron. All of these are also assimilated in the intestine to some degree.

The concentrations of specific ions in the gut are of particular interest because several of these, such as potassium, sodium and chloride, are important electrolytes in body fluids and digestive juices. To examine this, dry mass-specific values in Table 1 were converted from mg to mmol and then divided by gut water content to yield values in mmol/l (Fig. 2). In the stomach, both water content and chloride

TABLE 3. PROGRESSIVE CHANGES IN ESTIMATED COMPOSITION OF ONE GRAM (DRY MASS) OF INGESTED FOOD AS IT MOVES THROUGH THE GUT OF A CHUCKWALLA. Units indicate the amount of each substance remaining in the food bolus as it passes through each gut segment. See text for method of calculation.

	Food	Stomach	Sm. Intest.	Lg. Intest.	Rectum	% Assim.
Dry Matter, g	1.0	1.0	.62	.30	.31	69
Ash-free dry matter, g	.78	.75	.30	.11	.10	87
Water, ml	2.53	5.59	5.43	1.14	.58	77
Ash, mg	218.6	247.2	319.5	187.0	208.2	5
Nitrogen, mg	23.1	23.7	5.42	5.48	5.0	78
Potassium, mg	24.7	8.48	1.61	1.24	2.36	90
Sodium, mg	1.16	3.94	20.1	1.62	.21	82
Chloride, mg	6.56	30.28	7.29	.79	.98	85
Calcium, mg	27.8	13.0	11.4	9.98	8.87	68
Magnesium, mg	4.87	3.33	3.09	2.13	2.47	49
Iron, mg	.67	1.34	.97	.53	.55	18
Aluminum, mg	1.01	2.81	1.78	1.08	1.10	-9
Strontium, μg	204.3	126.5	113.0	80.2	73.6	64
Boron, μg	88.1	68.4	59.8	31.5	29.6	66
Copper, μg	7.3	8.1	4.9	4.9	3.7	49

concentration were higher than in the food, suggesting that hydrochloric acid was secreted onto the food. Further, stomach contents were quite acidic (Table 2). The 85% decrease in potassium concentration between food and stomach indicates that a great deal of dietary K^+ entered the body through the gastric mucosa. In the small intestine, sodium concentration increased markedly, and the pH was high (alkaline). This suggests that sodium bicarbonate and/or sodium bile salts were secreted into the small intestine. In the large intestine and rectum, the pH was about neutral, and water and sodium were reabsorbed. Chloride concentration in rectal contents was somewhat higher and potassium concentration was much higher than in the large intestine. The increase in potassium concentration in the hindgut was more than can be explained by the decrease in water content.

DISCUSSION

Cellulose digestion.—In a previous study (Nagy, 1972), untreated cotton (90% cellulose) that was force-fed to chuckwallas did not change mass after passing through the gut, indicating that cellulose was not digested. However, it turns out that most of the cellulose in cotton is in a

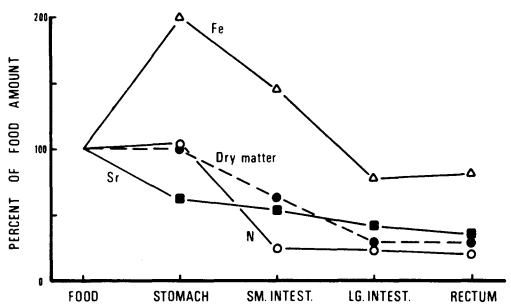

Fig. 1. Progressive changes in the composition of a food bolus that contained 1 g dry matter upon ingestion, as it moves through the gut of a chuckwalla. The iron (△), nitrogen (○), strontium (■) and dry matter (●) contents are plotted as percent of the amount in the initial food parcel (calculated from values in Table 2).

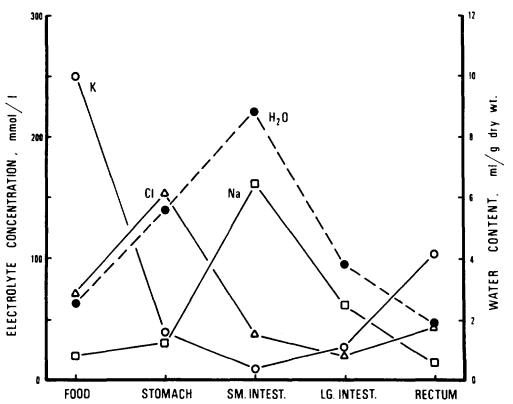

Fig. 2. Water content (●) and concentrations of potassium (○), sodium (□) and chloride (△) in food and in the contents of various parts of the digestive tract of chuckwallas.

crystalline form which is very resistant to enzymatic degradation (Cowling and Brown, 1969). Thus, cotton is probably a poor indicator for cellulose digestion. Present evidence indicates that chuckwallas have high levels of cellulolytic activity in their large intestines. Despite this, it appears that cellulose digestion is not of major importance in supplying energy to these lizards. If a significant fraction of cellulose was assimilated, this should have been detectable as a decrease in the ash-free dry matter content from large intestine to rectum. In fact, virtually all organic matter assimilation apparently occurred only in the small intestine (Table 3). McBee (1971) and Ziswiler and Farner (1972) cautioned that, although cellulolytic microbes have been found in the ceca of many plant-eating mammals and birds, there is little evidence that cellulose digestion is important to the energy balance of these animals.

The source of the cellulase in chuckwallas remains unknown. The measureable levels of enzyme activity in large intestine walls may indicate that this tissue was secreting cellulase, but it seems more likely that this activity resulted from residual contamination that was not removed by washing. The observation that nematodes in the large intestine contained a fair amount of activity may indicate that they produced the cellulase and secreted it into their environment. Alternatively, the worms simply could have eaten cellulase-containing digesta or cellulase-producing microorganisms. Several nematodes that are parasitic on plants are known to produce cellulases (Gascoigne and Gascoigne, 1960; Von Brand, 1973), but the occurrence of cellulases in nematodes inhabiting animals has not been established. Dubuis et al. (1971) found many worms in the ceca of another herbivorous lizard, *Uromastix acanthinurus*, and suggested that the worms may be important in these lizards' digestive processes.

Nutrient assimilation.—The food of chuckwallas contained relatively high levels of potassium and calcium, but sodium content was low, as is common in many desert plants (Wallace and Romney, 1972), but is in contrast to the diet of carnivores. Surprisingly large amounts of both potassium and calcium were absorbed in the stomach (Table 3). Excess potassium is excreted by the nasal salt glands, as well as in precipitated form in urinary pellets (Nagy, 1972), but the mechanism of calcium excretion is not known in lizards. In alligators, calcium loads are excreted in the feces, suggesting rectal or cloacal secretion of this ion (Dantzler and Holmes, 1974). Cloacal secretion of potassium, as suggested by Braysher and Green (1970) for a varanid lizard, may account for the increase in potassium concentration in the chuckwalla rectum (Fig. 1). Alternatively, urine that contained potassium could have been refluxed from the cloaca into the rectum, as occurs in birds (Ohmart et al., 1970). If the assimilated calcium is not excreted by cloacal walls in chuckwallas, then the kidneys may be very important in this regard.

In general, fractional assimilations of most dietary substances measured in this study are about the same as in mammals (Berger, 1960; Schroeder, 1973; Kaufman et al., 1976). The values for nutrient assimilation reported herein are only approximations, for several reasons. First, the actual (gross) assimilation of a substance may be much greater than these measurements indicate, because substances can reenter the gut lumen via diffusion or in secretions from digestive glands. Second, the relatively large variations in the measurements, as indicated by the standard errors in Table 1, and the small sample sizes for some gut segments (the probable explanation for the apparent secretion of some substances into the rectum, as indicated in Table 3), preclude precise descriptions of fractional assimilation. Third, accurate assimilation measurements require determination of the successive changes in a particular parcel of food as it moves through the gut. The results in this paper indicate the status of the gut contents of chuckwallas at the time of death only, and it is assumed that this is representative of the changes occurring in a particular food bolus with time.

General nature of chuckwalla digestion.—The results of this study can be used to examine the general pattern of digestive physiology in chuckwallas, and to compare it with those in plant-eating mammals (Moir, 1968; Barnard, 1973). Among herbivorous mammals, three arbitrary categories can be distinguished: ruminants, coprophagous non-ruminants, and non-ruminants that do not ingest their feces. Ruminants (cows, sheep, deer, elk, antelope) have enlarged, chambered stomachs. The first chamber (rumen) contains cellulolytic bacteria and the pH is near neutral. Here the sugars resulting from cellulose digestion are utilized by the microbes for growth. The host derives benefit from this situation primarily by assimilating the byproducts of sugar fermentation (volatile fatty acids), and by digesting and assimilating the microbes

as they pass on through the gut. The two categories of non-ruminants have smaller, simple stomachs, the contents of which are acidic as in carnivorous mammals, but the large intestines of these herbivores are greatly enlarged, may include a voluminous cecum, and harbor dense microbe populations which may produce cellulases. Although there is litle evidence that products of cellulose digestion are assimilated in significant quantities by the large intestine (McBee, 1971), it is generally accepted that other substances, including several vitamins and minerals, are liberated by the microbes and assimilated, thereby contributing greatly to the host's nutritional status. Those non-ruminants that are coprophagous (rabbits, hares and many rodents including beavers) derive additional nutrition by digesting the microbes themselves, much the same as do ruminants. The non-ruminants that do not reflect (horses, pigs, elephants) thereby lose the nutrients contained in the cells of cecal microorganisms.

Chuckwallas have simple, acidic stomachs and large intestines that are big and contain a cecum—quite similar to non-ruminant, herbivorous mammals. Moreover, chuckwallas are not known to eat their own feces, although occasional fecal pellets (mainly from rodents) are seen in their stomachs (Nagy, 1973). It appears, then, that the general nature of digestion and assimilation in these lizards is about the same as in relatively unspecialized mammalian herbivores.

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Osmoregulatory Seasonality and Freezing Avoidance in Some Fishes from a Subarctic Eelgrass Community

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Osmotic responses and seasonal movements of fishes in Izembek Lagoon, a shallow embayment of the Bering Sea, were studied. Twenty-three species were collected during the study. Seven of these were year-round residents while 4 other species occur there only in the summer. Seasonal movements may be into fresh water (*Gasterosteus aculeatus, Platichthys stellatus*) or offshore into deeper water (*Pholis laeta, Pallasina barbata, Hexagrammos octogrammus*). Four of the 7 year-round residents exhibited winter serum osmotic concentrations about 60% above summer values. The relative proportion of electrolytes decreased with increasing osmotic concentration, indicating the accumulation of additional nonelectrolyte compounds in the body fluids. Although osmotic adjustments were dramatic, either supercooling or migration was still necessary to survive winter ambient temperatures.

A number of investigations have dealt with the relationship of osmoregulation to freezing resistance in polar marine teleosts. Some Antarctic fishes of the genus *Trematomus*, which are constantly exposed to very cold water, have evolved a glycoprotein antifreeze which holds their freezing points (Δ_f) constant at or below that of the environment (Δ_o) (De Vries and Wohlschlag, 1969). Some Labrador fishes, which experience a seasonal temperature range of 6 C, are able to adjust their Δ_f values seasonally to more closely match winter Δ_o and thus lessen the probability of freezing (Scholander et al., 1957; Gordon et al., 1962). Some other recent studies have demonstrated osmotic adaptations to more extreme temperature fluctuations in the natural environment. These include a temperature range of –0.5 C to 17 C for sculpins from the Baltic (Raschack, 1959), a range of –1.5 C to 15 C for cod from the Berents (Eliassen et al., 1960) and a range of +2.5 C to 20.6 C for winter flounder from New Jersey (Umminger and Mahoney, 1972). Our study was initiated to look for evidence of freezing resistance in Alaskan shallow water subarctic marine fishes which experience a much greater seasonal range of ambient temperatures than do most previously studied fishes.

Our study site was Izembek Lagoon, near the tip of the Alaska Peninsula. This lagoon is a