J. Zool., Lond. (1992) **226,** 387–398

Microbial digestion in the herbivorous lizard *Uromastyx aegyptius* (Agamidae)

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(*Accepted 14 March 1991*)

(With 3 figures in the text)

The utilization of a diet rich in plant cell walls was studied in a large, desert-dwelling, herbivorous lizard, *Uromastyx aegyptius* (Agamidae). The diet eaten by *U. aegyptius* in spring in the 'Arava Valley, Israel, consisted almost entirely of leaves and fruits of short-lived annual plant species. The leaves contained only moderate levels of fibre compared with grasses and tree leaves, but those fruits eaten were markedly higher in fibre and lignin. All items had notably high contents of ash.

Following oral doses of [^{14}C] cellulose, $^{14}CO_2$ was detected in respired air from *U. aegyptius*, demonstrating that the cellulose was digested and that the lizards gained oxidative energy from cellulose degradation. The hind gut was the principal site of microbial activity and the apparent digestibility of the cell-wall fraction was 69%. Similarly, the caecum/proximal colon had the highest concentrations of SCFA (76–120 mM).

The mean rate of SCFA production at 40 °C *in vitro* was 31 mmol/l h^{-1}. Assuming that this is representative of daily production rate, 69 kJ/kg d^{-1} would be made available to the animal. This is 47% of the mean digestible energy intake estimated in free-living animals. Microbial fermentation contributes an important part of the energy budget of *U. aegyptius* but the effects of variation in body temperature on digestion and fermentation need further consideration.

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Introduction

Although relatively few reptiles subsist solely on plant tissues, there has been much interest in their energetics in recent years (Iverson, 1982; Nagy, 1982*a*; Troyer, 1984*a*). This is because herbivorous forms are amongst the largest members of several reptilian families (Pough, 1973) and because some of these inhabit desert areas where plant resources seem sparse. Also, herbivorous reptiles appear to lack some of the adaptations that have allowed mammalian herbivores to exploit fibrous diets. For example, herbivorous lizards do not chew their food and use the teeth solely to crop pieces from larger plant parts (Throckmorton, 1974). In spite of this, the apparent digestibility of dietary fibre in some species of herbivorous lizards is often surprisingly high (R. M. Hansen & C. K. Sylber, unpubl.; Andrews, 1984). Part of this can be attributed to end-point errors in determining faecal output due to the irregular and infrequent defecations of many species, but the long retention times found in herbivorous lizards (Guard, 1980; Troyer, 1984*b*) may provide sufficient time for extensive fibre degradation (Karasov *et al.*, 1986).

All herbivorous lizards have enlarged and partitioned hind guts where microbial digestion is presumed to take place (Iverson, 1982). Although high concentrations of short-chain fatty acids (SCFA) have been found in these organs in some species (e.g. *Iguana iguana*; Troyer, 1984*b*) there have been no reliable measurements of fermentation rate. Preliminary results of McBee & McBee (1982) suggested extensive fermentation in the hind gut of *I. iguana*. Assessment of the quantitative importance of microbial fermentation would seem then to be a first step in explaining the ability of herbivorous reptiles to digest plant cell walls.

Uromastyx aegyptius belongs to a genus of large burrow-dwelling agamid lizards found throughout the Middle East. It inhabits extreme desert areas and is almost entirely herbivorous (Kevork & Al-Uthman, 1972), at least as an adult. *Uromastyx aegyptius* has a simple stomach but the hind gut, in particular the caecum/proximal colon, is enlarged, suggesting a site of microbial fermentation (El Toubi & Bishai, 1959).

This paper reports the results of a study of the digestive physiology of free-living *U. aegyptius*. We wanted to know whether plant cell walls were an important part of the diet of *U. aegyptius*, whether cell-wall digestion followed a similar pattern to that in mammals and what contribution digestion of cell walls made to the animal's daily energy requirements.

Materials and methods

Study area

Field work was conducted in the 'Arava Valley, southern Israel (30° 47′ N, 35° 17′ E; elevation, (−)200 m). The average rainfall is 71 mm (Katsnelson, 1966), but this is very variable. Mean daily temperature of the hottest month (August) is 31·4 °C and of the coolest month (January) 13·8 °C. The vegetation is dominated by large shrubs of *Haloxylon persicum* and *Hammada salicornica* and is typical of wadis with deep sand. The perennial shrubs are accompanied by many annual psammophytes (e.g. *Plantago cylindrica* and *Savignya parviflora*) (Rudich & Danin, 1978).

Diet composition

The diet of *U. aegyptius* was determined from an analysis of the stomach contents of 8 animals killed in connection with other experiments described below from 27 March to 7 May 1986. Wildlife Service permits limited us to this sample size. Different plant species and parts were sorted and then dried to constant mass at

85 °C and their occurrence was expressed as a proportion of the total dry matter of the sample. Fresh specimens of these plants were then collected adjacent to burrows, freeze-dried and analysed for residual dry matter, organic matter, total nitrogen, cell-wall constituents and sodium and potassium, by standard methods (Goering & Van Soest, 1970; Allen, 1974).

Degradation of labelled cellulose

Three adult *U. aegyptius* (mean mass = 1570 g; SVL = 341 mm) were captured (Bouskila, 1985) and body temperature was determined immediately (mean = 39·9 °C). Each animal was given by stomach tube about 0·9 ml of [^{14}C] cellulose (about 0·3 MBq) suspended in 1% carboxymethylcellulose. The animals were then placed in an open-circuit respirometer on a 12 h/12 h day/night cycle for 24 h. Body temperatures were maintained at 40 °C during daytime conditions and at 34 °C during the night. Expired CO_2 was collected in KOH and later isolated as $BaCO_3$. The activity of [^{14}C] was determined by liquid scintillation spectrometry (Larsen, 1973).

Digestion and intake of food

The digestibility of the diet was determined by the manganese ratio technique. Manganese has proved to be a suitable indigestible marker in other herbivorous lizards (see, e.g. Nagy, 1977). Four *U. aegyptius* were killed by a cardiac injection of sodium pentabarbitone. Each section of the gut was weighed and the pH of the contents determined with narrow-range pH paper. Samples were freeze-dried to constant mass and analysed for residual dry matter, organic matter, neutral detergent fibre (NDF) and nitrogen content as described above. Manganese was determined by atomic absorption spectrometry.

Food intake was estimated by measuring the rate of water intake and the water content of the food. No free water was available in the study area and although unseasonal storms occurred during the study they did so when the animals were inactive in their burrows and no water remained on the surface when the animals became active. However, these storms limited our ability to recapture all marked animals and so we obtained only 3 measurements of water turnover. Diet items were collected adjacent to the burrows both before and after the storms and the water content was determined by desiccation to constant mass at 85 °C. Water intake was determined by using tritiated water and metabolic water production was estimated by fitting small muzzles to 2 animals according to the procedure of Nagy (1972).

Production of SCFA ***in vitro***

Four *U. aegyptius* were captured in mid-afternoon (mean $Tb = 39{\cdot}7$ °C; mean mass = 2310 g; mean SVL = 353 mm) and killed with a cardiac injection of sodium pentabarbitone and the gut was treated as described. Samples of digesta were taken from the stomach, small intestine, caecum and colon for determination of SCFA concentration and particle size distribution. The remainder of the caecal contents were used to measure SCFA production by an *in-vitro*, zero-time method (Carrol & Hungate, 1954). The average time from the death of the animal to the start of the incubations was 16 min.

SCFA and ethanol concentrations were measured by gas-solid chromatography (Carlsson, 1973) using iso-propanol as an internal standard. The proportion of particles of different sizes in the digesta was determined by the method of Evans *et al.* (1973).

Statistical

Analysis of variance was used to compare between means. Proportions were transformed with an arc-sine function before computation. Results are expressed per kg mass because of uncertainties about the appropriate scaling factors applicable to lizards.

Results

Diet and diet composition

Stomachs of *U. aegyptius* contained almost exclusively plant material (Table I) and the animals fed principally on short-lived annual plants. Although a total of 23 species were identified in the diet, more than 58% of the dry matter consisted of the leaves and fruits of *Plantago cylindrica*. Perennial plants (e.g. *Diplotaxis harra* and *Polycarpaea repens*) were only a minor proportion of the diet at this time of year.

Table I also gives details of the chemical composition of the major items consumed. Notable was the low water content of *P. cylindrica* fruits compared with the other plants and plant parts. The ash content of all items was high but this may result partly from contamination of the surfaces of the leaves with sand. The neutral detergent fibre (NDF) content of the leaves was only moderate (17–36%) as was the proportion of lignin in the NDF. In contrast, fruits of *P. cylindrica* and *Neurada procumbens* had markedly higher contents of NDF and lignin than did the leaves.

Degradation of labelled cellulose

$^{14}CO_2$ was detected in the expired air from all three animals dosed orally with [^{14}C] cellulose, indicating that cellulose was degraded and that the animals obtained oxidative energy from cellulose degradation. Figure 1 shows an example of the pattern of $^{14}CO_2$ excretion over time. The peak excretion was between 18 and 22 h after dosing. $^{14}CO_2$ continued to be produced throughout the night, which suggests that cellulose degradation took place at body temperatures of 34 °C as well as 40 °C.

Digestion and intake of food

The mean mass of digesta (expressed as a percentage of mean body mass) in each of the main segments of the gut is given in Table II. The caecum/proximal colon contained 11% of the total body mass and the entire gut contents were on average 19% of body mass.

Figure 2 shows the proportions of organic matter, NDF and total nitrogen remaining in different parts of the digestive tract. The manganese content of the diet was in all cases significantly greater ($P<0{\cdot}05$) than that in the anterior part of the stomach. Thus, in order to calculate apparent digestibility, we have taken the nutrient and manganese content of the digesta from the anterior part of the stomach as a starting point. The short time that elapsed between the last meal and death and the absence of chewing in these animals should mean that these values are close to those of the plants eaten. The hind gut was the principal site of apparent digestion of organic matter and cell walls. The mean apparent digestibility of organic matter was 80%, of cell-wall constituents 69%, and total nitrogen 84%.

The mean water influx rate was $25{\cdot}1 \pm 3{\cdot}2$ ml/kg d^{-1}. Tritium space was $68{\cdot}7 \pm 1{\cdot}0$% of body mass. The two muzzled animals had water influx rates of 6·0 and 4·5 ml/kg d^{-1} and the mean value was taken as an estimate of metabolic water production.

From the details of diet and plant water content given in Table I, mean dry-matter intake was estimated to be $10{\cdot}3 \pm 0{\cdot}7$ g/kg d^{-1}. The mean organic-matter intake was $8{\cdot}3 \pm 0{\cdot}5$ g/kg d^{-1} and the intake of cell walls was $4{\cdot}5 \pm 0{\cdot}5$ g/kg d^{-1}. Digestible energy intake (DEI) was estimated from the energy content of the diet and cloacal digesta. The mean DEI was 147 ± 9 kJ/kg d^{-1}.

TABLE I

Occurrence and chemical composition of plants eaten by ***U. aegyptius***

Species	Occurrence in diet (% DM)	Dry matter (% wet)	Organic matter (% DM)	NDF (% DM)	Hemi-cellulose (% DM)	Cellulose (% DM)	Lignin (% DM)	Total nitrogen (% DM)	Sodium (mmol/gDM)	Potassium (mmol/gDM)	Gross energy (kJ/gDM)
Plantago cylindrica (L)	24·1	27·6	73·7	33·8	11·6	18·5	3·7	2·19	0·10	0·43	15·0
Plantago cylindrica (F)	34·1	54·7	85·4	58·7	24·1	29·0	5·6	1·02	0·06	0·30	16·3
Savignya parviflora	5·0	29·1	81·5	37·1	9·6	21·9	5·6	2·30	0·10	0·48	17·4
Oligomeris subulata	4·5	29·4	87·3	30·4	8·9	15·7	5·8	2·87	0·13	0·91	19·3
Anthemis melampodina (R)	4·2	26·0	85·7	39·1	11·6	23·6	3·9	1·42	0·11	0·56	18·6
Neurada procumbens (L)	3·7	29·4	81·8	25·7	5·9	17·5	2·3	1·92	0·04	0·42	16·4
Neurada procumbens (F)	0·2	25·0	91·8	65·2	8·5	46·9	9·8	1·39	0·05	0·45	18·4
Diplotaxis harra (L)	1·9	18·3	62·6	17·3	3·5	12·5	1·3	2·33	0·43	1·00	12·0
Launaea mucronata (L, R)	1·7	23·9	87·1	36·6	10·8	21·7	4·1	2·14	0·18	0·74	18·8
Bassia muricata (L)	1·4	31·7	72·5	50·2	19·2	27·0	4·0	1·69	0·44	0·76	13·2
Erucaria boveana	0·9	19·5	79·3	20·6	6·3	12·0	2·3	2·77	0·46	0·75	18·2
Reseda arabica	0·3	24·3	85·5	30·5	6·9	16·7	6·9	2·97	0·04	0·79	17·6
Erodium bryoniifolium	0·3	35·5	90·5	30·3	7·4	16·5	6·4	2·03	0·06	0·32	17·9
Other species[a]/unknown	17·7	—	—	—	—	—	—	—	—	—	—

[a] *Arnebia decumbens*, *Trigonella stellata*, *Reichardia tingitana*, *Farsetia aegyptiaca*, *Schimpera arabica*, *Medicago laciniata*, *Launaea angustifolia*, *Polycarpaea repens*, *Malva parviflora*, *Gymnarrhena micrantha*, *Astralagus* sp., *Zygophyllum simplex*. Includes 3 insect pupae (< 3 mg) found in one stomach

L = leaves only, R = flowers only, F = fruits only

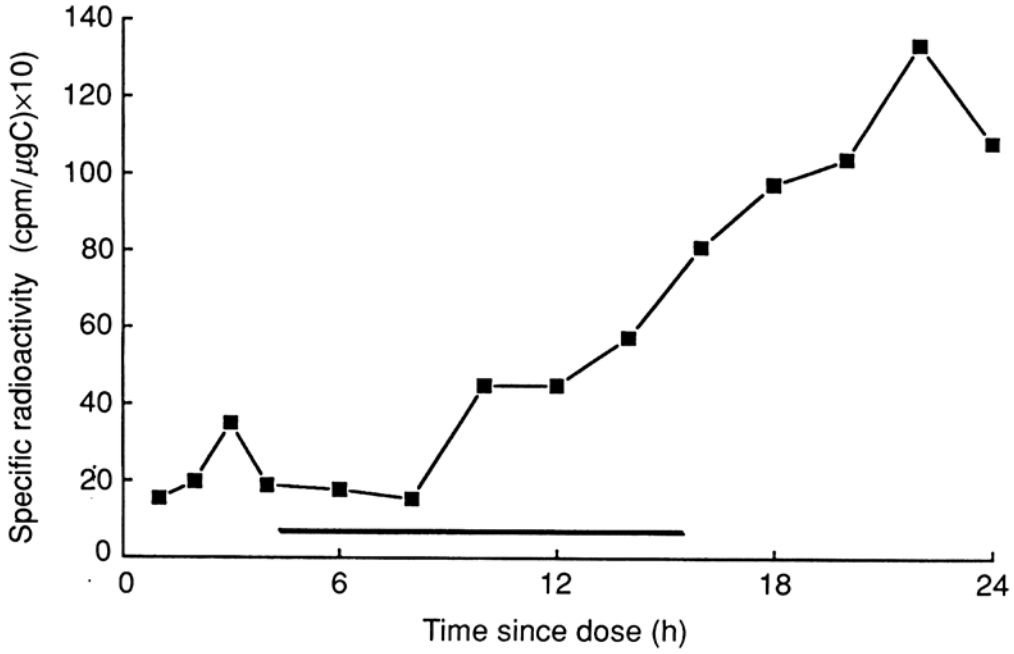

FIG. 1. Pattern of excretion of $^{14}CO_2$ from a *U. aegyptius* given an oral dose of [^{14}C] cellulose and maintained at a body temperature of 40 °C during daytime and 34 °C at night. Bar indicates duration of night conditions.

Production of SCFA

Details of the concentration and molar proportions of SCFA, the concentration of ethanol and pH in different parts of the gut of *U. aegyptius* are given in Table II. The concentration of SCFA was greater ($P<0{\cdot}001$) in the hind gut than in either the stomach or the small intestine. Similarly, SCFA concentrations were greater ($P<0{\cdot}001$) in the cranial parts of the caecum than in the proximal colon and rectum. In all parts of the gut, acetate was the principal fatty acid but the stomach and small intestine contained a notably high molar proportion of valerate (23–34%). Ethanol occurred in low concentrations in digesta from all parts of the gut and there were no significant differences between gut segments. The maximum ethanol concentration in the hind gut was 2·2 mM.

TABLE II

Digesta mass, pH, ethanol and short-chain fatty acids in different parts of the gut of ***U. aegyptius****. (Mean ± S.E.)*

	Digesta mass (% body mass)	pH	Ethanol (mM)	SCFA (mM)	Molar proportions (%)			
					Acetic	Propionic	Butyric	Valeric
Stomach								
anterior	4·9 ± 0·6	1·9 ± 0·3	1·47 ± 0·40	6·89 ± 1·02	62·7 ± 4·2	5·9 ± 2·4	0·0 ± 0·0	31·4 ± 3·2
posterior		1·8 ± 0·1	1·45 ± 0·29	12·97 ± 3·98	75·6 ± 3·4	1·3 ± 1·3	0·0 ± 0·0	23·3 ± 3·3
Duodenum		6·9 ± 0·1	1·73 ± 0·65	9·93 ± 2·05	65·6 ± 4·1	0·7 ± 0·7	8·3 ± 5·6	25·3 ± 3·7
Jejuneum	1·6 ± 0·2	7·0 ± 0·1	1·93 ± 0·50	7·55 ± 1·27	61·6 ± 1·9	0·0 ± 0·0	6·1 ± 4·6	32·3 ± 4·6
Ileum		7·1 ± 0·1	1·94 ± 0·67	5·71 ± 0·75	62·5 ± 4·7	0·0 ± 0·0	3·4 ± 1·8	34·2 ± 3·9
Caecum	7·3 ± 1·0	6·9 ± 0·1	1·72 ± 0·37	119·80 ± 3·00	79·4 ± 1·5	8·0 ± 0·4	9·9 ± 0·2	1·3 ± 0·2
Proximal colon	3·5 ± 0·4	7·0 ± 0·1	2·50 ± 0·82	76·44 ± 6·36	74·7 ± 1·0	9·5 ± 0·7	13·0 ± 1·2	1·1 ± 0·0
Distal colon	1·1 ± 0·2	7·1 ± 0·1	1·20 ± 0·26	59·91 ± 9·38	75·0 ± 0·8	9·4 ± 0·3	12·5 ± 0·3	1·0 ± 0·1

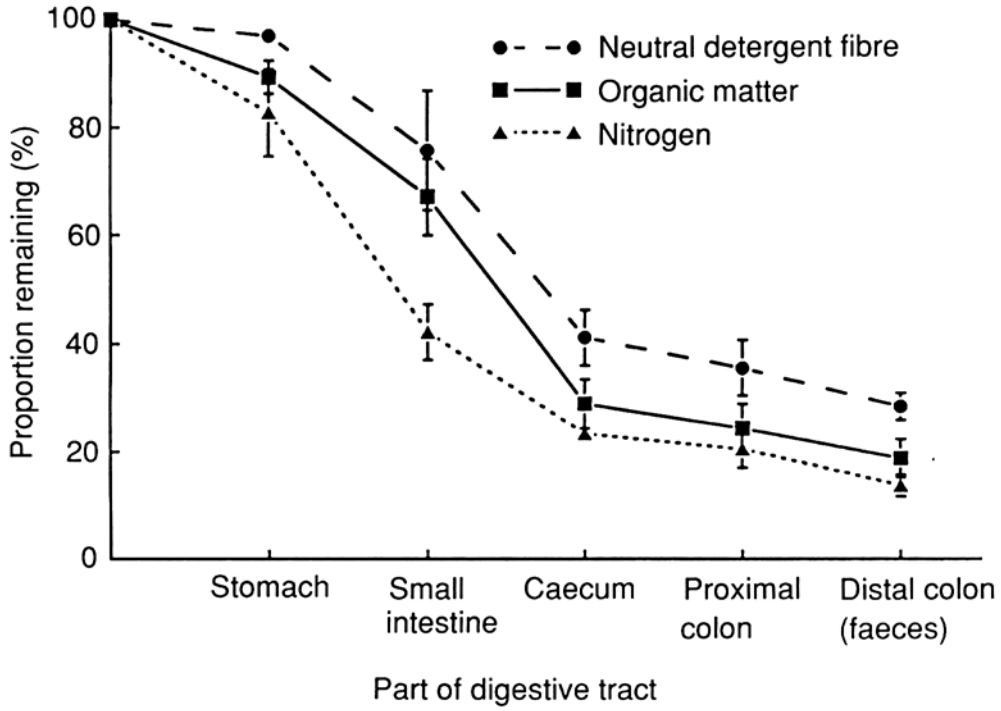

FIG. 2. Proportion of organic matter, cell-wall constituents (NDF) and nitrogen remaining in the different parts of the gut of *U. aegyptius*. Mean ± S.E. ($n = 4$).

Table III gives details of the rates of production of individual fatty acids. Production rates were linear in almost all cases but in one animal a smooth curve could not be fitted to the valeric acid data and so no production rate could be estimated. The mean rate of production of total SCFA was 31·1 mmol/l digesta fluid h^{-1} or 148 mmol/g digesta dry matter h^{-1}. Acetic acid accounted for 79% of the total SCFA production whereas propionic and butyric acids accounted for 9% and 10%, respectively. There was no significant difference between the initial molar proportion of these three fatty acids and their contribution to total SCFA production. This suggested that no fatty acid was preferentially absorbed.

The daily production of SCFA was estimated from the production rates of individual fatty acids and the volume of digesta in the hind gut and assuming that production rates measured at 40 °C represent daily production (see **Discussion**). These data are given in Table IV. The mean rate of SCFA production was 62 mmol/kg d^{-1}.

TABLE III

Rates of production of individual SCFA (mmol/l digesta fluid min^{-1}) in the caecum and proximal colon of ***U. aegyptius in vitro*** *at 40 °C. (Mean ± S.E.; $n = 4$)*

Acid	Production rate	% Total	Initial molar %
Acetic	0·409 ± 0·091	78·7	79·7 ± 1·0
Propionic	0·050 ± 0·007	9·6	9·0 ± 0·3
iso-butyric	0·001 ± 0·001	0·2	0·9 ± 0·4
Butyric	0·053 ± 0·008	10·2	8·3 ± 1·6
iso-valeric	0·003 ± 0·002	0·6	0·6 ± 0·2
Valeric[a]	0·004 ± 0·002	0·8	1·5 ± 0·2

[a] $n = 3$: no production rate could be calculated for Animal 4

TABLE IV

Daily production of short-chain fatty acids in the caecum and proximal colon of ***U. aegyptius*** *at 40 °C* ***in vitro***

	Lizard				
	1	2	3	4	Mean ± S.E.
Body mass (kg)	3·65	2·00	2·06	1·53	2·31 ± 0·46
SVL (mm)	403	332	348	329	353 ± 17
Digesta mass (g)	363	242	164	152	230 ± 48
Digesta DM (%)	22·8	15·9	13·3	17·6	17·4 ± 2·0
Production of SCFA					
(mmol/l h^{-1})	46·5	36·0	23·4	18·6[a]	31·1 ± 6·3
(mmol/kg d^{-1})	85·7	88·1	38·7	36·6	62·3 ± 14·2
(kJ/kg d^{-1})	91·1	98·9	43·4	41·5	68·7 ± 15·3

[a] Valeric acid production not included (see text)

Digesta particle size

Details of the distribution of different-sized digesta particles in the gut of *U. aegyptius* are given in Fig. 3. There were fewer ($P < 0{\cdot}001$) large ($> 2{\cdot}0$ mm) particles in the caecum and faeces than in the stomach. However, there were no significant differences in the proportions of different-sized particles between the digesta in the caecum and the rectum. There was thus no evidence of preferential retention of fine particles in the hind gut.

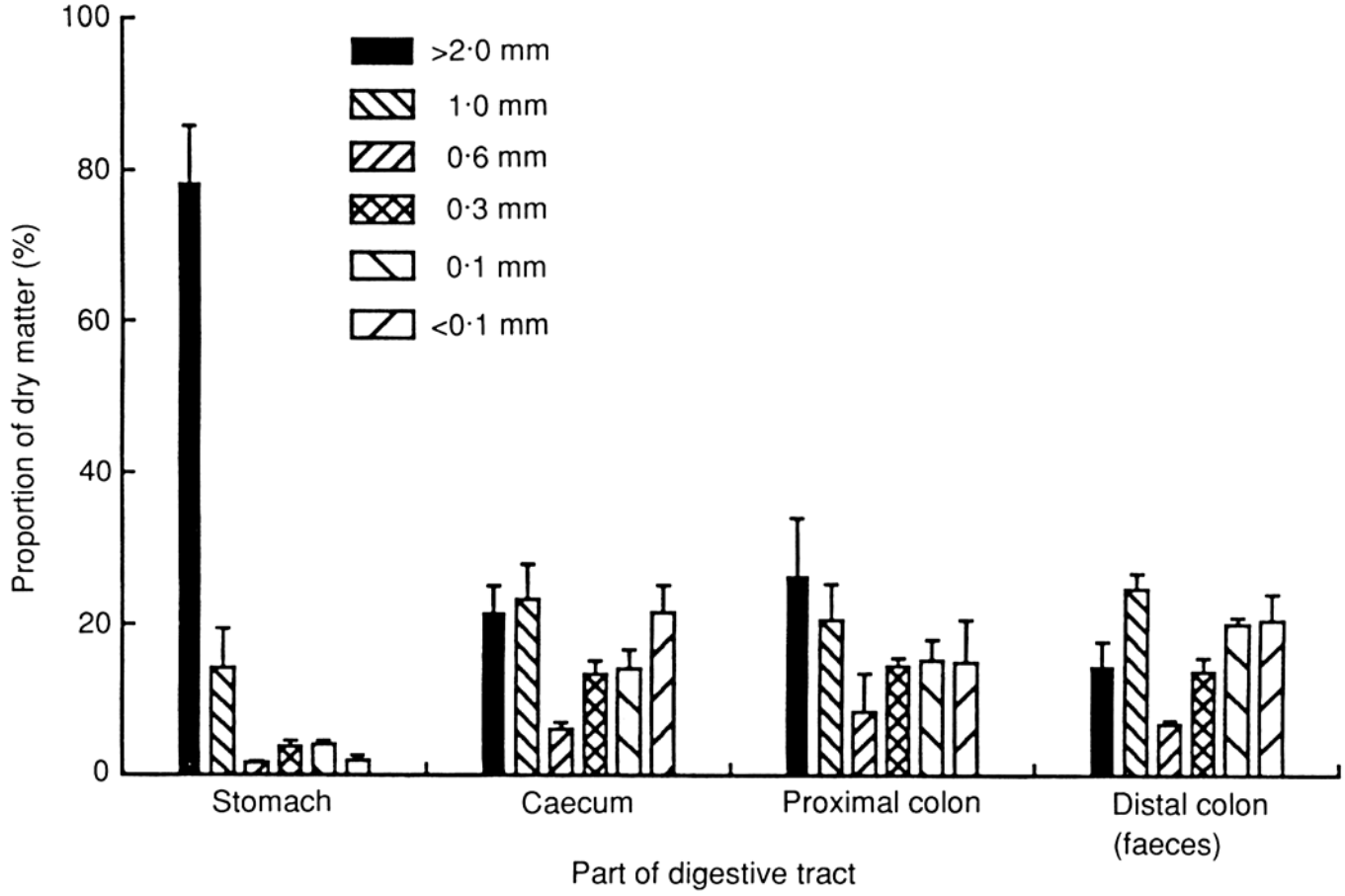

FIG. 3. Proportion of digesta from different parts of the gut of *U. aegyptius* which were retained on sieves of varying sizes. Mean ± S.E. ($n = 4$).

Discussion

Uromastyx aegyptius is a generalist herbivore feeding on plants close to its burrow in the spring (Bouskila, 1986). In this study, we identified 23 species of plants in the stomach contents. Other studies of *U. aegyptius* (Kevork & Al-Uthman, 1972) and of other *Uromastyx* species (e.g. *U. acanthinurus*; Lemire, Grenot & Vernet, 1982) have similarly identified a large range of plant species in the diet.

The fibre content of the most favoured plants is moderate in comparison with grasses and tree leaves (Van Soest, 1982). None the less, more than 58% of a *P. cylindrica* fruit consists of cell-wall material. However, since the cell walls of *P. cylindrica* are not highly lignified they are potentially highly digestible.

Studies with labelled cellulose showed that at least this part of the cell-wall fraction can be degraded by *U. aegyptius*. Evolution of $^{14}CO_2$ implies that the [^{14}C] cellulose has been digested and the animal has obtained oxidative energy from the metabolic products of digestion. $^{14}CO_2$ could result from the oxidation of absorbed fatty acids but could also be a by-product of microbial fermentation. None the less, the pattern of $^{14}CO_2$ excretion suggested that [^{14}C] cellulose was being degraded when the lizard's body temperature was 34 °C as well as at 40 °C. $^{14}CO_2$ was detected within 2 h of dosing the animal with [^{14}C] cellulose and the peak excretion occurred 18–22 h after dosing. This is considerably faster than the digesta retention times recorded in *U. aegyptius* (Throckmorton, 1974) and is most likely due to the rapid passage of fluid digesta through the tubiform stomach (Guard, 1980).

Several lines of evidence suggested that the caecum/proximal colon was the principal site of microbial activity and thus of cellulose digestion. First, the concentrations of SCFA were significantly higher in the caecum/proximal colon than in other parts of the gut. Secondly, the hind gut was the principal site of apparent disappearance of organic matter and cell-wall constituents. Finally, electron microscopy (W. J. Foley, unpubl.) revealed micro-organisms attached to plant particles only in the caecum and colon and not in the stomach. Our estimates of organic matter and NDF digestion are high, 80% and 69%, respectively. However, these values are comparable to values found in other herbivorous lizard species fed fresh plant tissue (e.g. *Egernia cunninghami*: Andrews, 1984; *Conolophus* spp.: Christian, Tracy & Porter, 1984).

The concentration of SCFA in the stomach of *U. aegyptius* was similar to that found in the stomachs of hind gut-fermenting mammals and in *I. iguana* (Troyer, 1984*b*) and *Chelonia mydas*, the green turtle (Bjorndal, 1979). However, the low pH of the stomach digesta of *U. aegyptius* suggests that little active fermentation takes place. The very high molar proportion of valerate found in the stomach was unusual and may have arisen as a constituent of one of the ingested plants.

The concentration of SCFA in the caecum/proximal colon was again similar to that found in the hind gut of most herbivorous mammals (Engelhardt & Rechkemmer, 1983), *I. iguana* (Troyer, 1984*b*) and *C. mydas* (Bjorndal, 1979). Production rates of SCFA were comparable to those found in some mammalian herbivores (e.g. wallabies: Hume, 1982) but faster than those measured in arboreal marsupials fed highly lignified tree foliage (Foley, Hume & Cork, 1989). Production rates were about three times greater than those measured in the hind gut of a single *C. mydas* by Bjorndal (1979).

The pattern of component SCFAs, with acetate forming the vast majority, is typical of mammalian fermentations of high-fibre substrates. In contrast, McBee & McBee (1982) found that butyrate was the major SCFA produced in the hind gut of *I. iguana*. Fermentation rate in

U. aegyptius is probably ultimately limited by lignified tissues but also by the large amount of ash in the diet, since, in these experiments, ash formed between 30 and 40% of the mass of the hind gut contents.

The majority of SCFA produced in the hind gut of *U. aegyptius* was apparently absorbed since faecal excretion of SCFA was less than 2% of the estimated daily production of SCFA. However, it was surprising that there was no evidence of preferential absorption of any SCFA. In many mammalian herbivores and in the green turtle (Bjorndal, 1979), SCFAs are absorbed at rates directly related to their chain length and there seems little reason to suspect that the situation should be different in herbivorous lizards. Interconversion of SCFA, in particular the formation of butyrate from acetate, may be the reason for the present results.

Our estimate of food intake and thus digestible energy intake (DEI) should be treated cautiously since it is based on so few observations of water turnover. Similarly, it is possible that plants took up water rapidly after the unseasonal storms so that the water content of the plants collected did not represent that which the animals ate. However, we collected plants adjacent to the burrows both before and after the storms and our estimates of water turnover are close to those predicted from the allometric equations of Nagy (1982*b*). In the absence of other data, we believe that it is reasonable to estimate the importance of SCFA in the daily energy budget of *U. aegyptius* by comparing the energetic equivalent of SCFA (Table IV) with the estimated daily DEI.

If it is assumed (see discussion below) that the mean SCFA production rate measured is representative of production rates throughout the whole day, then SCFA represents about 47% of the daily DEI of *U. aegyptius*. This reflects the moderate production rate of SCFA in the hind gut but also the large volume of digesta in the caecum/proximal colon. It is clear that microbial fermentation contributes significantly to the energy intake of *U. aegyptius* and allows the animals to continue to acquire metabolic energy while avoiding lengthy foraging and the consequent risk of predation (Bouskila, 1986). However, the balance of daily energy requirements must be met from the digestion of cell contents. Since *U. aegyptius* does not chew its food (Throckmorton, 1974), we do not know how the cell walls are ruptured to release the contents.

The assumption that production rates measured at 40 °C are representative of daily production needs to be interpreted cautiously. Fermentation rates in herbivorous lizards may be affected by the supply of fermentable substrate and by the temperature at which the fermentation proceeds. Additionally, SCFA production rates estimated *in vitro* usually underestimate *in-vivo* production in mammalian herbivores.

The effect of temperature on digestion in herbivorous lizards remains uncertain since most data have been obtained from animals that were force-fed to varying levels (Andrews, 1984; Zimmerman & Tracy, 1989). None the less, both Andrews (1984) and Zimmerman & Tracy (1989) concluded that there was little effect of temperature on digestibility of dry matter or cell-wall constituents but that passage rates were significantly slower at lower body temperatures.

Slower digesta passage rates have been suggested as being one of the major differences in digestive function between herbivorous lizards and hind gut-fermenting mammals (Karasov *et al.*, 1986). However, this comparison is confounded by basic differences in digesta flow between the two groups. The little available evidence in reptiles (Guard, 1980) suggests that the fluid fraction of the digesta passes rapidly through the digestive tract with the particles being retained. However, in many small hind gut-fermenting mammals (Bjornhag, 1987), it is the fluid fraction which is retained and coarse particles are rapidly excreted. The question thus becomes one of methodology and comparisons made between mammals and reptiles using markers of just one digesta fraction, as has been done in the past, may be insufficient to identify the real differences.

This study has shown that fermentation can make a major contribution to the intake of energy by herbivorous lizards. However, the interrelationships between temperature, fermentation and digesta passage have yet to be elucidated satisfactorily. The study of these aspects should be a priority in future studies of the digestive physiology of herbivorous reptiles.

We wish to thank the Society for Protection of Nature in Israel for the use of facilities at Hazeva Field Study Centre and for financial support of A.B. W.J.F. was supported by a postdoctoral scholarship from Tel-Aviv University. Dr A. Shmida (Hebrew University, Jerusalem) identified many of the plants for us and Dr D. Ben-Ghedalia (Volcani Institute) and Dr C. Dosoretz (MIGAL) kindly allowed several of the analyses to be carried out in their laboratories. We thank Mr D. Levanon for excellent technical assistance.

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