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Diet quality does not affect resting metabolic rate or body temperatures selected by an herbivorous lizard

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Abstract Diet quality can influence many aspects of digestion, but the links between diet quality and resting metabolism are poorly understood. In nature, it might be beneficial to reduce energy expenditure when only poor quality diets are available. Alternatively, animals might increase the processing capacity of the gut to more thoroughly extract energy. If maintaining the processing capacity of the gut is energetically expensive, then increasing gut size or function might result in higher resting metabolism. In ectotherms, most digestive functions are temperature dependent, thus another strategy to maintain energy balance might be to alter selected body temperatures. We tested whether differing concentrations of dietary fiber affected the resting metabolic rate or body temperatures selected by chuckwallas (*Sauromalus obesus*) – lizards that naturally experience marked variation in dietary fiber. Resting metabolic rates measured at two temperatures and over three time intervals did not differ between groups of lizards force-fed low- (30% neutral-detergent fiber; NDF) and high-fiber (45% NDF) diets, nor did these diet differences influence body temperatures selected in a thermal gradient. We conclude that ecologically relevant differences in diet quality may have negligible effects on resting metabolic rates and body temperatures selected by chuckwallas.

Key words Diet quality · Herbivory · Resting metabolic rate · *Sauromalus obesus* · Thermoregulation

Abbreviations *ADF* acid-detergent fiber · *BMR* basal metabolic rate · *NDF* neutral-detergent fiber · *RMR* resting metabolic rate · T_{sel} selected body temperature

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Introduction

The effects of diet quality on food intake and digestibility have been well studied – particularly in herbivorous endothermic vertebrates – but curiously the effects of diet quality on basal and resting metabolism are poorly known. Moreover, the influence of diet quality on basal and resting metabolism is difficult to predict from either an evolutionary or a proximate physiological perspective. McNab's (1986) research on among-species differences in basal metabolism of mammals suggests that mammals eating low-quality foods might evolve lower rates of basal metabolism. If basal and field metabolic rates of mammals are correlated (Koteja 1991), a reduction in basal or resting metabolic rate (BMR and RMR, respectively) might result in a concomitant reduction in daily energy expenditure. Such a reduction in daily energy expenditure would be advantageous to an animal that is having difficulty meeting its energetic requirements on low-quality foods (McNab 1986). While this line of reasoning is based on among-species differences acquired over evolutionary time, at least two recent intraspecific studies reported decreases in basal metabolism when mammals were fed low-quality foods (Veloso and Bozinovic 1993; Koteja 1996). These two studies demonstrate that at least some vertebrates have evolved the ability to respond at the proximate physiological level to changes in diet quality.

The ability of some species of vertebrates to alter BMR or RMR in response to diet quality should not be surprising because other proximate mechanisms for reducing RMR are well known. For example, when food quality or availability is reduced, many endotherms use torpor or estivate, and many ectotherms hibernate or select a lower body temperature when diet quality is poor (Gregory 1982; Lyman et al. 1982; Smits 1985).

Despite the data supporting the ability of two species of mammals to alter BMR as a proximate response

to diet quality, the generality of this response is far from clear. An alternative proximate response to feeding on low-quality diets might be to increase RMR as a result of a compensatory, and presumably costly (Brugger 1991; Secor et al. 1994), increase in gut capacity and perhaps function. Higher fiber diets clearly cause increases in gut size in herbivorous rodents (Gross et al. 1985; Green and Millar 1987; Hammond and Wunder 1991; Castle and Wunder 1995; Campbell and MacArthur 1996; Koteja 1996), and this increase in gut size may be metabolically costly (Webster 1981; Secor et al. 1994; Konarzewski and Diamond 1995). While no data exist for herbivorous ectotherms, a reduction in diet quality might be expected to elicit a similar response.

Although digestion, metabolism, and thermoregulation have been studied in ectotherms for decades (reviewed in Espinoza and Tracy 1997), few studies have examined the interactions among these three variables generally, and to our knowledge none have addressed the effects of diet quality on the energetics of an herbivorous ectotherm specifically. We examined the effect of a high-fiber diet on resting metabolism and body-temperature selection in an herbivorous lizard, the chuckwalla (*Sauromalus obesus*). Chuckwallas live in desert environments where, owing to variable rainfall patterns, they eat plants that vary in fiber content both seasonally and annually (Nagy 1973; Nagy and Shoemaker 1975; Abts 1987; Zimmerman 1989; Zimmerman and Tracy 1989). Hence, we hypothesized that chuckwallas might have acquired traits that compensate for potential energetic deficits when only high-fiber foods are available.

Materials and methods

Resting metabolic rate

Animals and their care

Juvenile chuckwallas were captured in the deserts of the southwestern United States in 1993 and raised in captivity (Tracy 1995). We received the animals in 1995 as adults. Lizards were kept in small groups (6–8) of similarly sized individuals and housed in metal troughs (2.0 × 0.6 × 0.4 m) in a greenhouse at the University of Nevada, Reno. Fluorescent UV lights provided a 12:12 photocycle, and opportunities for thermoregulation were provided by two 150 W heat lamps positioned over each trough. Troughs were lined with 2.5 cm of sand, and plastic pipes provided refugia. Lizards were fed moistened guinea pig chow (alfalfa pellets) 3 times per week. The chow was supplemented weekly with vitamins and bone meal, and water was available ad libitum.

In March 1996, we randomly assigned 27 male chuckwallas (females are typically gravid at this time) to either the high-fiber (n = 14) or low-fiber (n = 13) diet treatment. Initial body masses did not differ between the two groups (high-fiber mean = 223.2 g; low-fiber mean = 226.9 g; t = 0.24; P = 0.81). The lizards were placed into individual plastic containers (24 cm^2 × 10 cm). Each container was covered with a wire-mesh lid and lined with a plastic 1 cm^2 grate that prevented the lizards from contacting or ingesting their feces. The containers were placed in a constant-temperature cabinet maintained at 32 °C (±1.0 °C) with fluorescent UV lights providing a 12:12 photoperiod.

Diets and diet analyses

The low-fiber diet was prepared by grinding alfalfa pellets (Farmer's Best guinea pig chow) in a commercial coffee mill. The manufacturer's analysis of the low-fiber diet indicated that it contained not less than 16.0% protein; 2.7% fat; and not more than 13.5% crude fiber. We created the high-fiber diet by mixing additional fiber into the low-fiber diet. Unground low-fiber diet (~700 g) was enclosed in a muslin bag, washed in a washing machine 3 times with unscented laundry detergent (Tide Free), rinsed through five wash cycles, dried for 2 days at 45 °C, and ground as for the low-fiber diet. The high-fiber diet was produced by mixing one part of the washed chow with two parts of the low-fiber diet.

The diets were analyzed for neutral- and acid-detergent fiber (NDF and ADF, respectively) using Zimmerman's (1989) modification of Van Soest and Robertson's (1985) technique. NDF approximates the proportion of the diet containing hemicellulose, cellulose, and lignin. ADF approximates the cellulose and lignin fraction. Digestible fiber is determined by subtracting the mass of the ADF fraction from the NDF fraction because hemicellulose is generally digestible by vertebrates with symbiotic gut microflora (Stevens 1988; Hammond and Wunder 1991). The high-fiber diet contained significantly more NDF ($\bar{x}$ = 45.2%, SD = 1.4) and ADF ($\bar{x}$ = 25.6%, SD = 0.4) than the low-fiber diet (NDF: $\bar{x}$ = 30.2%, SD = 0.5; ADF: $\bar{x}$ = 19.6%, SD = 2.2). Furthermore, the NDF fractions of the experimental diets were within the range of those measured by Zimmerman (1989) for plants eaten by chuckwallas in nature (NDF: 29.5–53.1%). The ADF concentration of our high-fiber diet was about mid-range (estimated from data in McArthur et al. 1994) relative to foods eaten by chuckwallas in nature (Shaw 1939; Johnson 1965; Nagy 1973, 1977; Nagy and Shoemaker 1975; Zimmerman 1989; Zimmerman and Tracy 1989).

Feeding

Photophase started at 0700 hours and the animals were fed between 1000–1100 hours. This schedule generally allowed enough time for the lizards to become active and to defecate before feeding. Prior to feeding, the body mass of each lizard was recorded. Diets were prepared fresh for each feeding by mixing dry chow 1:7 (by volume) with warm water and blending for 30 s with an electric mixer. This ratio was required to facilitate gavaging, and is not an uncommon proportion for plants eaten by chuckwallas in nature (Nagy 1973). We estimated a maintenance ration for each lizard from Zimmerman (1989; eq. 1). After 1 week of force feeding, the body masses of the lizards were stable. Thereafter, the quantity of food was adjusted, when necessary, to ensure that the body mass of the individual lizards did not change over the course of the experiment. The animals were force-fed by oral gavage and the amount fed was recorded as the difference in the body mass of the lizard before and after feeding.

Measurements of resting metabolic rate

We measured resting oxygen consumption at two ecologically relevant temperatures (30 and 40 °C ± 0.5 °C). Pre-treatment RMR measurements were made at both experimental temperatures 2 days prior to initiating the diet manipulations. Post-treatment measurements were taken after the lizards had been fed the experimental diets for 2, 4, and 5 weeks. Oxygen consumption was measured at one temperature per day. All measurements were made between 1100–1600 hours local time, and after at least 24 h had elapsed since the last feeding. Each lizard was measured once at each temperature for a given time interval (i.e., 2, 4, and 5 weeks).

Oxygen consumption was measured via closed-system respirometry (Vleck 1987) following the techniques described by DeVera and Hayes (1995) which are slight modifications of standard methods (see e.g., Chappell 1984a, b; Morgan et al. 1985; Chappell and Morgan 1987). We used closed-system respirometry because it enabled us to obtain simultaneous measurements of a large number

of lizards and circumvented the problems associated with measuring RMR in animals over different parts of their circadian cycle (Aschoff and Pohl 1970; Bennett 1972; Burggren 1997). Lizards were placed in glass jars (1890 ml for two smaller lizards, 2702 ml for all others) capped with wire-mesh lids and placed in an environmental chamber. Lizards were allowed to acclimate to the chamber for at least 30 min. After acclimation, we replaced the screen lids with air-tight lids fitted with inlet and outlet valves. After an additional 5 min, the air in the jars was mixed by pumping a 60 ml syringe connected to the inlet 5 times while both the inlet and outlet valves were open. Immediately after mixing, an initial air sample (60 ml) was collected, both valves were closed, and the time was recorded. The lizards remained in the jars for 30 min. During this time, we observed the animals through a window at 1 min intervals to determine if they remained at rest. Lizards that moved were not included in the analyses. Consequently, sample sizes varied from 6–13 ($x = 11$) individuals per treatment group per measurement period (Table 1). After approximately 30 min, the inlet tube was connected to a 60 ml syringe, its valve opened, and the gas in the jar mixed by repeatedly pumping the syringe (5 times) with the outlet valve closed. Immediately after mixing, we collected a final 60 ml sample of gas and recorded the time.

Oxygen concentration of the air samples was determined with an Ametek S-3A/II dual-channel oxygen analyzer that was operated in differential mode. The analyzer was used in differential mode (i.e., set to record differential oxygen concentration) because it measures differential concentration more accurately than it measures absolute fractional concentration. The analyzer was plumbed as follows. Starting from the upstream end, there was a long piece of narrow plastic tubing open to room air. The downstream end of the tubing was connected to a small tube containing Drierite, Ascarite, then more Drierite (to remove water and carbon dioxide, respectively). Downstream of the Drierite and Ascarite, the tubing was connected to the inlet port of the first channel of the oxygen analyzer. Air was pulled through the sensor with a downstream precision flow controller (i.e., pump) set at 95 ml/min. An identical set up was connected to the second channel of the oxygen analyzer. Upstream of the Drierite and Ascarite in the second channel set up, a needle was inserted pointing upstream. The connection of the needle to room air was closed with a two-way valve. Gas samples were injected into the tube leading to sensor (channel) two of the analyzer. The sample was injected by hand at a faster rate (i.e., 120 ml/min) than the air was drawn into the sensor by the downstream pump. The tubing was open on the upstream end to prevent the induction of a pressure change which would affect the reading obtained on this type of oxygen analyzer. Because the rate of injection of the gas sample (120 ml/min) exceeds the rate at which air is drawn from the tube into the analyzer (95 ml/min), the sample is injected as a bolus of gas into the tubing. This bolus of gas is then drawn into the sensor. The injection resulted in a leading edge of gas that contained a mix of sample and room air, followed by a bolus of sample air (unmixed with room air), and a trailing edge of gas that contained a mix of sample and room air. The procedure was validated by injecting reference gases with known oxygen concentration into the system and confirming that the sample oxygen concentration was accurately measured.

We used DataCan V software (Sable Systems, Salt Lake City) to record the difference in oxygen concentration between control channel and the air sampled from the jars containing the lizards. Samples were recorded at 0.5 s intervals. Injected air samples typically resulted in a rapid rise in differential oxygen concentration, followed by a plateau, and then a rapid return to ambient oxygen concentrations. The differential oxygen concentration was then subtracted from 0.2095 to obtain the actual oxygen concentration. Rate of oxygen consumption was calculated according to Vleck (1987; Eq. 9). We estimated the volume of air in the jars by subtracting the volume displaced by each lizard (assuming 0.98 g = 1 ml; De Vera and Hayes 1995) from the volume of water that the jar could hold. We assumed that the initial fractional concentrations of water vapor and carbon dioxide in the jars were zero (Vleck 1987). These assumptions are not strictly valid but our analyses of initial gas concentrations (sensu Vleck 1987) indicate that our method resulted in overestimates of oxygen consumption that averaged 0.5% or less (maximum error 1.1%). All estimates of oxygen consumption were corrected to standard temperature and pressure (0 °C; 101325 Pa) and are reported as ml O_2/h.

Data analyses

We compared RMR between the low-fiber and high-fiber groups using a one-factor ANCOVA (SuperANOVA: Abacus Concepts, Berkeley Calif.), where diet was the treatment and body mass was the covariate. Each temperature (30 and 40 °C), and time interval (2, 4, and 5 weeks) was analyzed separately.

We calculated the repeatability of oxygen consumption by individuals to obtain an indication of the consistency the RMR measurements. Repeatability was assessed by product-moment correlations and partial (i.e., mass-adjusted) correlations of metabolic rate across time and temperatures.

Selected body temperatures

Animals and their care

In August 1996, we randomly assigned 24 male chuckwallas (of the 27 used for the RMR measurements) to either the high- or low-fiber diet. The lizards were housed in four metal troughs (six individuals per trough) as described above. Each morning the animals were provided with the appropriate diet (mixed 1:3 with water) ad libitum. A lower water concentration was used in this experiment than in the RMR experiments because the lizards were fed ad libitum, and higher water contents made the food difficult for them to eat. The body masses of the lizards stabilized within 3 weeks and experiments began immediately thereafter.

Thermal gradient

A thermal gradient (2.4 × 0.6 × 0.5 m) was constructed of plywood with an aluminum floor covered by 2–3 cm of sand. One end of the gradient was heated (via electrical resistance) from the underside using three circuits of wires connected in series. Each circuit was

Table 1 Body mass of chuckwallas over the course of the resting metabolic rate experiments. Mean mass (g) for each group over each measurement interval, with the number of individuals (*n*) included in each analysis

Temperature	Week	Low fiber		High fiber	
		Mass (±1 SD)	*n*	Mass (±1 SD)	*n*
30 °C	0	224.2 (25.3)	8	216.7 (69.4)	6
	2	226.9 (20.3)	10	232.2 (55.4)	8
	4	238.8 (33.2)	12	229.3 (50.4)	12
	5	229.0 (23.9)	12	227.1 (53.7)	11
40 °C	0	223.7 (25.2)	10	219.1 (43.9)	11
	2	229.1 (22.1)	11	196.7 (103.0)	12
	4	208.6 (65.5)	13	227.5 (52.6)	12
	5	235.2 (20.9)	11	226.5 (52.4)	12

connected to a dimmer switch which permitted independent control of temperature for the three sections of the gradient. The opposite end of the gradient was cooled by chilled water (4–6 °C) that circulated continuously through copper coils fixed to the underside of the gradient floor. The gradient provided a range of substratum temperatures from 17 to 60 °C. A 12:12 photoperiod (0700–1900 hours) was provided by two fluorescent UV lights suspended 0.7 m above the gradient. A 4 W light 0.7 m above the gradient provided diffuse illumination and mitigated the abrupt darkness at the onset of scotophase. The gradient was divided into three equal lanes with aluminum flashing so the selected body temperature (T_{sel}) of three animals could be recorded simultaneously.

After feeding on the morning before the day T_{sel} were recorded, three lizards were randomly assigned to lanes and acclimated to the gradient for approximately 24 h. The following morning the lizards were offered their respective diets ad libitum and their body masses were recorded following the cessation of feeding (usually within 1 h). A 30 ga type-K thermocouple was then inserted approximately 2 cm into the cloaca and secured to the base of the tail with vinyl tape. Thermocouples were inserted into fine polyethylene tubing that reduced the likelihood of the lizards entangling themselves in the wire. The thermocouples were suspended above each lane of the gradient on paper clips which traveled freely on a fine steel wire thereby permitting each lizard to move unhindered. The animals were inspected several times throughout the day to ensure that the thermocouple did not become entangled or come out of the cloaca.

The signal delivered by the thermocouples was linearized and amplified with an analog amplifier (TAC80B-K; Omega Inc., Stamford, Conn.), and T_{sel} were collected every 2.5 min for approximately 24 h with a MacLab/4 (ADInstruments, Mass) interfaced to a computer running Chart software. Prior to the experiments, we compared the temperatures measured by each channel in the system (one for each lane) with those measured by a National Bureau of Standards (NBS) mercury thermometer. Over a range of 15–60 °C, all channels remained within 0.5 °C of the temperatures measured by the NBS thermometer. Body masses of the lizards were recorded after each trial. All measurements were made within a 5 week period to avoid the possibility of seasonal changes in T_{sel} (Case 1976).

Data analyses

For each individual, the mean T_{sel} was calculated separately for photophase (1300–1800 hours) and scotophase (2200–0300 hours). These time intervals were chosen a priori and reflect segments of the active and inactive periods, respectively. They exclude periods near the transition between light and dark and times when the animals were handled. Within these time intervals, interruptions in data collection occasionally occurred due to entanglements or removal of the thermocouple from the cloaca and due to equipment malfunctions. Five lizards from the high-fiber treatment and six from the low-fiber group were re-tested because of these complications. To be included in analyses, a minimum of 75% (225 min) of the T_{sel} data had to be collected during the predefined time periods. Eleven chuckwallas on the high-fiber diet and ten on the low-fiber diet satisfied these criteria for both photo- and scotophase. All lizards remained within 10% of their initial body mass (high fiber: $\bar{x} = -5.0\%$, SD = 2.1; low fiber: $\bar{x} = -4.5\%$, SD = 2.4) over the day that T_{sel} was recorded.

The mean T_{sel} were compared separately for photophase and scotophase. Inspection of the data determined that they were not normally distributed, therefore a Mann-Whitney test was used to compare T_{sel} between the treatment groups (Zar 1996).

Results

Resting metabolic rates

After an initial adjustment period of approximately 5 days, all lizards remained within 5% of their initial body mass for the remainder of the study (Table 1). For these lizards 5% change in body mass is not more than that produced by a single defecation.

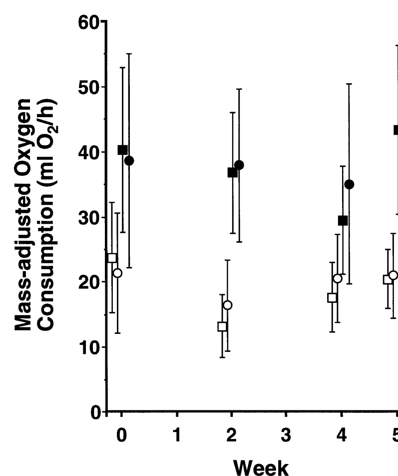

Fig. 1 Comparison of the resting metabolic rates (RMR; mean ± 1 SD) for the two diet treatment groups. The RMRs recorded for chuckwallas fed low- and high-fiber diets were statistically indistinguishable at both temperatures. Low-fiber (*squares*); high-fiber (*circles*) and 30 °C measurements (*unfilled*); 40 °C measurements (*filled*). Sample sizes are given in Table 1

There was no significant difference in RMR between the treatment groups prior to the dietary manipulation. Further, no significant differences in RMR were found between dietary groups at any measurement period at either temperature (Fig. 1). Our estimates of RMR and their variances were similar to those recorded by other investigators for chuckwallas and other similarly sized herbivorous lizards (Boyer 1967; Bennett 1972; Pough 1973; Wilson and Lee 1974; Nagy and Shoemaker 1975; Nagy 1982; Zari 1991, 1996). In general, product-moment and partial correlations revealed that measurements of RMR were repeatable across measurement periods and between temperatures.

Selected body temperatures

When combined for the two diet treatments, the mean T_{sel} of chuckwallas in the thermal gradient (photophase = 36.9 ± 1.4 °C, n = 23; scotophase = 36.9 ± 4.4 °C, n = 22) were similar to those recorded for this species in other laboratory and field studies (e.g., Case 1976, 1982; Zimmerman and Tracy 1989; Muchlinski et al. 1990). However, the differences in the T_{sel} of chuckwallas in this experiment were statistically indistinguishable between the two diet groups during both photophase and scotophase (photophase: U = 0.98; scotophase: U = 0.17; Fig. 2). Three animals fed the high-fiber diets selected notably cooler body temperatures during scotophase (Fig. 2). In nature, chuckwallas may exhibit individualistic patterns of nocturnal T_{sel} that are conserved over a season (Muchlinski et al. 1990). Thus, the low T_{sel} of the three individuals fed the

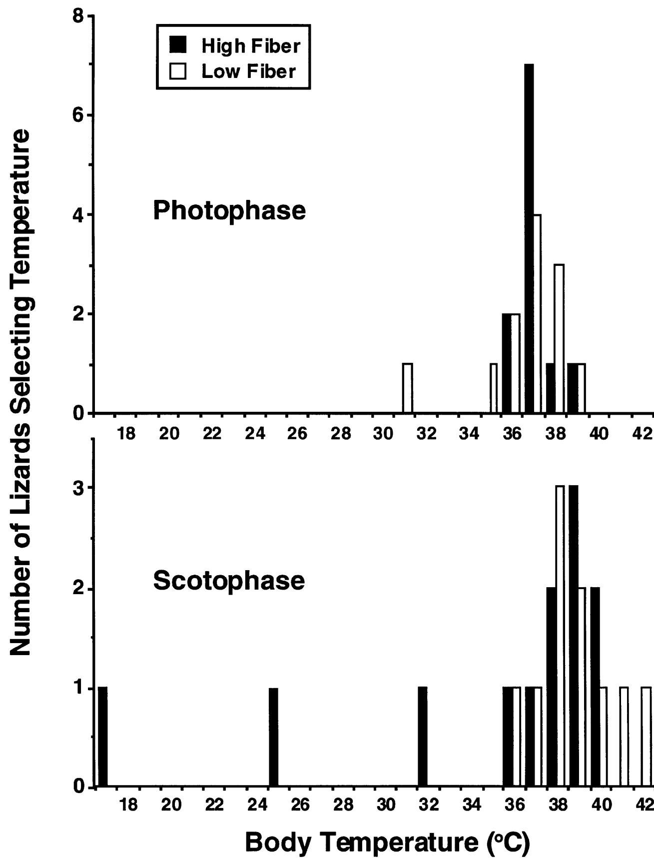

Fig. 2 Frequency of selected body temperature T_{sel} between chuckwallas fed high- and low-fiber diets. T_{sel} of chuckwallas fed low- and high-fiber diets were statistically indistinguishable during both photophase and scotophase. See text for discussion of outliers

high-fiber diet might be explained by individual preferences for particular nocturnal T_{sel} ranges. Nevertheless, this increased the overall variance in T_{sel} for this group, and thereby reduced the power of the dietary comparison ($1-\beta = 0.24$). Yet even if these individuals are excluded from the analysis, the variance in T_{sel} during scotophase is still higher than that measured during photophase.

Discussion

We hypothesized that a decrease in diet quality might result in up- or downregulation of RMR and a reduction in T_{sel}. However, we found no evidence for any of these hypothesized effects.

Animals that commonly experience low-quality diets might be expected to have the capacity to downregulate their metabolism, conserve energy, and thereby survive periods when the quantity or quality of food is reduced. There is evidence that species of mammals that feed on low-quality diets may have lower BMRs than species that feed on higher quality diets. For example, after analyzing the BMRs of eutherian mammals from different dietary guilds (e.g., insectivores, browsers, folivores), McNab (1986) suggested that mammals that ate foods with less accessible energy had evolved lower BMRs to survive periods of reduced food quality and availability (but see Harvey et al. 1991). This argument can be extended to suggest that animals might also proximately lower BMRs in response to seasonal changes in diet quality. Indeed, recent studies indicate that the proximate effects of diet on BMR warrant further study.

Veloso and Bozinovic (1993) found that degus (*Octodon degus*) fed high-fiber diets had lower BMRs than those fed diets low in fiber. They suggested that their results were consistent with McNab's (1986) predictions, but were operating at a proximate level. Similarly, other investigators have found that increases in dietary fiber elicited a reduction in BMR (or standard metabolic rate), or had no effect on BMR in other small rodents (Choshniak and Yahav 1987; Yahav and Choshniak 1990; Koteja 1996), and in the European starling (*Sturnus vulgaris*; K. Geluso, personal communication). Our results provide no support for a proximate effect of diet quality on RMR or on T_{sel} in this herbivorous lizard.

At least two digestive strategies may permit chuckwallas to maintain their RMR when confronted with foods that vary in quality. First, gut size may have increased but without a measurable increase in RMR. This increase could occur if the size of the metabolically costly region of the gut (see Konarzewski and Diamond 1995) remained constant and growth was restricted to relatively inert tissues. A larger gut capacity would increase the retention time and thereby enhance digestive efficiency (Sibly 1981; Stevens 1988). However, if only relatively inert tissue proliferated, there might be no increase in RMR. Further, the large intestines of chuckwallas harbor a community of microsymbionts that hydrolyze the cell-wall fraction of plant tissues, thereby releasing volatile fatty acids and energy stored in these structural components (Nagy 1977). Because volatile fatty acids do not require active transport to be assimilated (Johnson 1994), it is possible that increasing dietary fiber would not elicit changes that are reflected in metabolic requirements of the gut. Such a scenario may be especially relevant for herbivorous lizards that may acquire a substantial portion of their energy from fermentation by gut microsymbionts (McBee and McBee 1982; Troyer 1984; Foley et al. 1992).

Second, the fiber concentrations fed to these lizards may not have elicited an increase in gut size. There are at least two ways in which energy balance could be maintained without increasing gut size. First, an animal fed a high-fiber diet might adopt a "skimmer" digestive strategy (sensu Sibly 1981) – wherein the majority of the indigestible components of the diet are simply passed through the gut while the readily digested cell solubles are assimilated. Under these conditions, we would not expect an increase in gut size or resting metabolism. This assumes that a favorable energy balance can be main-

tained on the cell-soluble fraction of the diet and that digesta moves through the gut at a sufficient rate. Given that most of the lizards in the T_{sel} portion of this study did indeed select high body temperatures – both by day and at night – passage rates and assimilation efficiency of cell solubles were likely operating near peak levels (see Zimmerman and Tracy 1989).

Finally, while the NDF composition of our laboratory diets was comparable to the range found in nature, the ADF measurements may not have been different enough to elicit a metabolic or thermoregulatory response. If the ADF fraction is that portion of the NDF fraction that remains after passage through the acidic foregut, then the difference in the ADF fraction may be more influential to digestion in the hindgut. Consequently, the smaller difference between the ADF – rather than in NDF fraction – may have reduced the effective magnitude of the dietary differences. Future studies addressing the effects of fiber on the energetics of herbivores should examine the individual effects of the NDF and ADF fractions of the diet as well as differences between endotherms and ectotherms.

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References

Abts ML (1987) Environment and variation in life history traits of the chuckwalla, *Sauromalus obesus*. Ecol Monogr 57: 215–232

Andrews RM, Pough FH (1985) Metabolism of squamate reptiles: allometric and ecological relationships. Physiol Zool 58: 214–231

Aschoff J, Pohl H (1970) Rhythmic variations in energy metabolism. Fed Proc Physiol Soc Am 29: 1541–1552

Bennett AF (1972) The effect of activity on oxygen consumption, oxygen debt, and heart rate in lizards *Varanus gouldii* and *Sauromalus hispidus*. J Comp Physiol 79: 259–280

Boyer DR (1967) Interactions of temperature and hypoxia on respiration and cardiac responses in the lizard, *Sauromalus obesus*. Comp Biochem Physiol 20: 437–447

Brugger KE (1991) Anatomical adaptation of the gut to diet in red-winged blackbirds (*Agelaius phoeniceus*). Auk 108: 562–567

Burggren, WW (1997) Identifying and evaluating patterns in cardiorespiratory physiology. Am Zool 37: 109–115

Campbell KL, MacArthur RA (1996) Seasonal changes in gut mass, forage digestibility, and nutrient selection of wild muskrats (*Ondatra zibethicus*). Physiol Zool 69: 1215–1231

Case TJ (1976) Seasonal aspects of thermoregulatory behavior in the chuckawalla, *Sauromalus obesus* (Reptilia, Lacertilia, Iguanidae). J Herp 10: 85–95

Case TJ (1982) Ecology and evolution of the insular gigantic chuckawallas, *Sauromalus hispidus* and *Sauromalus varius*. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes Public, Park Ridge, NJ, pp 184–212

Castle KT, Wunder BA (1995) Limits to food intake and fiber utilization in the prairie vole, *Microtus ochrogaster*: effects of food quality and energy need. J Comp Physiol B 164: 609–617

Chappell MA (1984a) Temperature regulation and energetics of the solitary bee *Centris pallida* during intermale mate competition. Physiol Zool 57: 215–225

Chappell MA (1984b) Thermoregulation and energetics of the green fig beetle (*Cotinus texana*) during flight and foraging behavior. Physiol Zool 57: 581–589

Chappell MA, Morgan KR (1987) Temperature regulation, endothermy, resting metabolism, and flight energetics of tachinid flies (*Nowickia* sp.). Physiol Zool 60: 550–559

Choshniak I, Yahav S (1987) Can desert rodents better utilize low quality roughage than their non-desert kindred? J Arid Environ 12: 241–246

De Vera L, Hayes JP (1995) Repeatability of oxygen consumption in *Gallotia galloti*. J Herp 29: 151–154

Espinoza RE, Tracy CR (1997) Thermal biology, metabolism, and hibernation. In: Ackerman LJ (ed) The biology, husbandry and health care of reptiles. Vol 1. Biology. TFH Public, Neptune City, NJ, pp 159–194

Foley WJ, Bouskila A, Shkolnik A, Choshniak I (1992) Microbial digestion in the herbivorous lizard *Uromastyx aegyptius* (Agamidae). J Zool Lond 226: 387–398

Green DA, Millar JS (1987) Changes in gut dimensions and capacity of *Peromyscus maniculatus* relative to diet quality and energy needs. Can J Zool 65: 2159–2162

Gregory PT (1982) Reptilian hibernation. In: Gans C, Pough FH (eds) Biology of the reptilia, vol 13. Academic Press, New York, pp 53–154

Gross JE, Wang Z, Wunder BA (1985) Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. J Mammal 66: 661–667

Hammond KA, Wunder BA (1991) The role of diet quality and energy need in the nutritional ecology of a small herbivore *Microtus ochrogaster*. Physiol Zool 64: 541–567

Harvey PH, Pagel MD, Rees JA (1991) Mammalian metabolism and life histories. Am Nat 137: 556–566

Johnson LR (1994) Physiology of the gastrointestinal tract, 3rd edn. Raven Press, New York

Johnson SR (1965) An ecological study of the chuckwalla, *Sauromalus obesus* Baird, in the western Mojave Desert. Am Midl Nat 73: 1–29

Konarzewski M, Diamond J (1995) Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 49: 1239–1248

Koteja P (1991) On the relation between basal and field metabolic rates in birds and mammals. Funct Ecol 5: 56–64

Koteja P (1996) Limits to the energy budget in a rodent *Peromyscus maniculatus*: does gut capacity set the limit? Physiol Zool 69: 994–1020

Lyman CP, Willis JS, Malan A, Wang LCH (eds) (1982) Hibernation and torpor in mammals and birds. Academic Press, New York

MacArthur ED, Sanderson SC, Webb BL (1994) Nutritive quality and mineral content of potential desert tortoise food plants. Research Paper INT-473. Ogden Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 26p.

McBee RH, McBee VH (1982) The hindgut fermentation in the green iguana, *Iguana iguana*. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes Public, Park Ridge, NJ, pp 77–83

McNab BK (1986) The influence of food habits on the energetics of eutherian mammals. Ecol Monogr 56: 1–19

Morgan KR, Shelley TE, Kimsey LS (1985) Body temperature regulation, energy metabolism, and foraging in light-seeking and shade-seeking robber flies. J Comp Physiol B 155: 561–570

Muchlinski AE, Hogan JM, Stoutenburgh RJ (1990) Body temperature regulation in a desert lizard, *Sauromalus obesus*, under undisturbed field conditions. Comp Biochem Physiol 95A: 579–583

Nagy KA (1973) Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. Copeia 1973: 93–102

Nagy KA (1977) Cellulose digestion and nutrient assimilation in *Sauromalus obesus*, a plant-eating lizard. Copeia 1977: 355–362

Nagy KA (1982) Energy requirements of free-living iguanid lizards. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes Public, Park Ridge, NJ, pp 49–59

Nagy KA, Shoemaker VH (1975) Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. Physiol Zool 48: 252–262

Pough FH (1973) Lizard energetics and diet. Ecology 54: 837–844

Secor SM, Stein ED, Diamond J (1994) Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. Am J Physiol 266: G695–G705

Shaw CE (1939) Food habits of the chuckwalla, *Sauromalus obesus*. Herpetologica 1: 53

Sibly RM (1981) Strategies of digestion and defecation. In: Townsend CR, Calow P (eds) Physiological ecology: an evolutionary approach to resource use. Sinauer, Saunderland, Mass, pp 109–139

Smits AW (1985) Behavioral and dietary responses to aridity in the chuckwalla, *Sauromalus hispidus*. J Herp 19: 441–449

Stevens CE (1988) Comparative physiology of the vertebrate digestive system. Cambridge University Press, NY

Tracy CR (1995) Determinants of variation in body size among chuckwalla (*Sauromalus obesus*) populations. Unpublished MS thesis, University of Oklahoma, Norman, Okla

Troyer K (1984) Structure and function of the digestive tract of a herbivorous lizard *Iguana iguana*. Physiol Zool 57: 1–8

Van Soest PJ, Robertson JB (1985) Analysis of forages and fibrous foods. Laboratory manual for animal science 613, Cornell University, Ithaca, NY

Veloso C, Bozinovic F (1993) Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology 74: 2003–2010

Vleck D (1987) Measurement of O_2 consumption, CO_2 production, and water vapor production in a closed system. J Appl Physiol 62: 2103–2106

Webster AJF (1981) The energetic efficiency of metabolism. Proc Nutr Soc 40: 121–128

Wilson KJ, Lee AK (1974) Energy expenditure of a large herbivorous lizard. Copeia 1974: 338–348

Yahav S, Choshniak I (1990) Response of the digestive tract to low quality dry food in the fat jird (*Meriones crassus*) and the levant vole (*Microtus guentheri*). J Arid Environ 19: 209–215

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, Upper Saddle River, NJ

Zari TA (1991) The influence of body mass and temperature on the standard metabolic rate of the herbivorous desert lizard, *Uromastyx microlepis*. J Thermal Biol 16: 129–133

Zari TA (1996) Effects of body mass and temperature on standard metabolic rate of the herbivorous desert lizard *Uromastyx philbyi*. J Arid Environ 33: 457–461

Zimmerman LC (1989) Thermal effects on digestion in lizards: ecological implications for herbivorous ectotherms. Unpublished PhD Dissertation, Colorado State University, Fort Collins, Colo

Zimmerman LC, Tracy CR (1989) Interactions between the environment and ectothermy and herbivory in reptiles. Physiol Zool 62: 374–409

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