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Herbivory Imposes Constraints on Voluntary Hypothermia in Lizards

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Animals that are unable to meet their metabolic needs should adopt compensatory behaviors to mitigate their energetic deficits. Voluntary hypothermia is one such energy-saving strategy. Physiological constraints associated with the digestion of plant tissues, however, may limit the thermoregulatory options of herbivorous ectotherms. In this laboratory study, selected body temperatures of Desert Iguanas (*Dipsosaurus dorsalis*), subjected to two different rations of a carnivorous and a herbivorous diet, were measured in a laboratory thermal gradient. Lizards fed a carnivorous diet and rationed to 50% of their daily energetic requirement selected significantly lower body temperatures than did lizards in the other diet/ration treatments. Lizards fed a herbivorous diet selected higher body temperatures than did the same lizards fed a carnivorous diet regardless of ration. Our study indicates that selected temperatures are influenced by both diet quality and quantity. These results support the hypothesis that herbivorous reptiles require elevated body temperatures to digest plant tissues. Our findings do not fully support the behavioral hypothermia hypothesis, which posits that diurnal lizards will seek cool temperatures at night to reduce their energy expenditure. Thermoregulatory strategies of Desert Iguanas and other herbivorous lizards may be influenced by the need to balance high body temperatures to digest plant material with the high metabolic costs of maintaining high temperatures.

VOLUNTARY hypothermia, selecting cool microsites in a heterogeneous thermal environment to reduce body temperature, is well documented in many lizard species (Huey, 1982; Underwood, 1992; Angilletta and Werner, 1998) and has been hypothesized to be an energy-conserving strategy that can be adopted by reptiles during periods of inactivity (Regal, 1967). Reducing energy expenditure should be adaptive in desert environments where food resources can be seasonally limited and energetic costs can be high because of high environmental temperatures (e.g., Case, 1976; Zimmerman and Tracy, 1989; Zari, 1996).

The efficacy of voluntary hypothermia in attaining energy balance appears to depend upon both diet and an animal's energetic state. For example, when fed less food than required to meet metabolic needs, carnivorous Collared Lizards (*Crotaphytus collaris*) selected cooler temperatures at night compared to temperatures selected by fully fed lizards (Barnes, 1989; Sievert, 1989). Herbivorous lizards, in contrast, appear to require high body temperatures to digest plant diets (Troyer, 1987; Zimmerman and Tracy, 1989; van Marken Lichtenbelt, 1992). Digestive efficiency is relatively thermally independent in carnivorous and herbivorous lizards (Waldschmidt et al., 1986; van Marken Lichtenbelt, 1992). Passage time, however, is thermally dependent (Waldschmidt et al., 1986; van Marken Lichtenbelt, 1992), and food passage takes longer and has a higher thermal minimum in herbivores than in carnivores (Zimmerman and Tracy, 1989). Digestion in herbivores, therefore, is more thermally constrained than in carnivores. For herbivores, then, the benefits of sustained digestion at high body temperatures may outweigh the associated increase in metabolic costs. Consequently, herbivorous lizards should select high body temperatures throughout the day and night regardless of the amount of food consumed.

We tested the competing hypotheses that food-limited lizards should reduce body temperature to conserve energy and that herbivores should regulate to high body temperatures to maintain digestion by measuring body temperatures selected by Desert Iguanas (*Dipsosaurus dorsalis*) fed different diets and rations in a laboratory thermal gradient. These lizards were force-fed a carnivorous or herbivorous diet that either exceeded or was insufficient to meet their metabolic needs. Specifically, we tested the hypotheses that (1) diet quantity (percent of maintenance needs) and (2) diet quality (carnivorous or herbivorous) would influence temperature selection by these diurnal herbivorous lizards.

MATERIALS AND METHODS

Experimental animals and their husbandry.—We studied Desert Iguanas (*D. dorsalis*) because, although they are principally herbivorous (Norris, 1953; Mautz and Nagy, 1987), they also consume some animal matter in nature (Minnich and Shoemaker, 1970; Stebbins, 1985) and can thrive on carnivorous diets in captivity (pers. obs.). Adult Desert Iguanas ($N = 6$; mean ± 1 SD body mass = 69.1 ± 2.6 g), were collected from the Mojave Desert near Twentynine Palms, California (34°09′N, 116°03′W). For approximately two months before experiments began, lizards were maintained in the laboratory on a diet of lettuce, carrots, mixed vegetables, boiled eggs, and canned dog food and provided water ad libitum. Before and between experiments, the animals were housed in enclosures (1.15 × 1.20 × 0.75 m) with a sand substratum and access to elevated perches. In these cages, lizards were provided a 12:12 photoperiod via two 150-W incandescent flood lamps positioned 0.75 m above the sand. Lizards maintained body mass and appeared to be in good health at the time of the experiments.

Experimental apparatus and procedures.—Body temperatures were measured in a thermal gradient (2.40 × 0.45 × 0.65 m) that was equally partitioned lengthwise to allow two lizards to be tested simultaneously, one individual per lane (see Barnes, 1989; Nussear et al., 1998; Simandle et al., 2001). Substratum temperatures in the gradient were maintained by five electric heating coils on one end and one copper cooling coil containing circulating refrigerated water (~4 C) on the opposite end. The floor of the gradient was lined with 2 cm of sand, and substratum temperatures were recorded at 15-min intervals by eight thermocouples (Cu-Cn, 24 ga) placed at 30-cm intervals beneath ~0.5 cm of sand. Substratum temperatures were monitored during experiments to ensure that a constant and gradual thermal gradient was maintained along the length of the testing arena. Temperatures on opposite ends of the gradient ranged from 10–60 C. A black plastic blind surrounded the gradient to isolate lizards from occasional ambient disturbances (Sugerman, 1980). The gradient was illuminated on a 12:12 photoperiod by two 40-W fluorescent lamps suspended 1 m above the gradient floor. The gradient was also continuously illuminated with a 4-W tungsten bulb (''night light'') so that the testing arena was never totally dark.

Body temperatures of the lizards were measured by duct taping a thermocouple (Cu-Cn, 30 ga) to the chest of each lizard and covering the tip of the thermocouple with styrofoam (approximately 1 cm^2 in area and 0.5 cm thick) to insulate the thermocouple from the substratum. To verify the corresponence between chest and cloacal temperatures, we simultaneously measured these temperatures for an individual placed in different locations along the thermal gradient. Insulated chest temperatures correlated well with cloacal temperatures (Chest temperature = 1.503 × cloacal temperature −15.541, $r^2 = 0.99$; Flack, 1991). Body temperatures reported here are chest temperatures transformed to core temperatures. Measuring chest temperature avoided potentially confounding factors associated with water loss during long-term temperature recording through the cloaca. Chest temperatures were recorded every 15 min throughout the experiment using a Campbell® CR5 Digital Recorder data logger. Trials were interrupted each morning for about 3 min while the animals were fed.

Lizards were fed by oral gavage once daily at approximately 0900 (3 h into photophase). The herbivorous diet was Ralston Purina® (St. Louis, MO) high-fiber rabbit chow (HF 5326) that had 6.69 kJ/g in the neutral detergent fiber fraction (40.9% NDF) and 9.62 kJ/g in cell solubles (14.5% protein, 1.7% fat, 8.9% ash, 42.4% N-free extract, ~10% vitamins). The NDF and cell soluble fractions were estimated to be 50% and 90% digestible, respectively (Zimmerman, 1989). Hence, approximately 12.0 kJ/g were available to animals fed the herbivorous diet. The carnivorous diet of Friskies® (Carnation Company, Los Angeles, CA) liver and chicken cat food (nearly 100% digestible) had approximately 24.3 kJ/g of available energy (15% protein, 5% fat, 1% fiber, 2.5% ash). Both diets contained 80% water by mass. Desert Iguanas were acclimated to experimental diets (herbivorous or carnivorous) for at least two weeks prior to trials. Animals were acclimated to the experimental rations (50 or 150% of maintenance) for six days prior to the experiments. Lizards were weighed daily to the nearest 0.1 g during the acclimation period to determine the appropriate amount of food required to maintain them on a particular diet ration (Appendix 1).

Experimental design.—Lizards were subjected to four experimental treatments, in which the animals were fed (1) 50% or (2) 150% of the daily energetic requirement of a high-fiber herbivorous diet, and (3) 50% or (4) 150% of the daily energetic requirement of the carnivorous diet. The amount of food fed to a 69.1 g individual (mean body mass of lizards in this study) in each of the diet/ration treatments was 13.5 g/day (herbivorous/150%), 4.5 g/day (herbivorous/50%), 6.7 g/day (carnivorous/150%), and

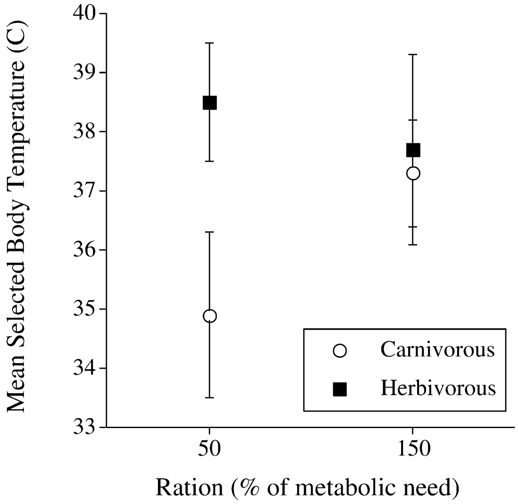

Fig. 1. Mean selected body temperatures (T_{sel}; ± 1 SD) during the day and night of lizards fed 50% and 150% rations. Lizards fed 50% of maintenance on the carnivorous diet had significantly lower ($F_{1,39}$ = 13.47, P = 0.0007) T_{sel} both during the day and at night (36.8 ± 1.1 C, and 33.0 ± 1.8 C, respectively), than did lizards in the three other treatment groups (150% carnivorous: 38.3 ± 0.8 C day, and 36.4 ± 1.4 C night; 50% herbivorous: 39.3 ± 1.2 C day, and 37.6 ± 1.9 C night; 150% herbivorous: 39.2 ± 0.7 C day, and 36.3 ± 0.8 C night).

2.2 g/day (carnivorous/50%). Daily energetic requirements were estimated using an equation from Andrews and Pough (1985), along with estimates of energy expenditures and reported body temperatures (Appendix 1; see also Nussear et al., 1998).

In this repeated-measures or within-subjects design, six Desert Iguanas were subjected to each of the four experimental treatments, beginning with the herbivorous diet. Animals were randomly assigned to either the low or the high ration, allowed to acclimate as previously stated and then run in the gradient. Rations were switched, and these animals were run again in the gradient following acclimation to the ration. After the experiments with herbivorous diets, lizards were given a two-month hiatus, after which the second half of the experiment with the carnivorous diet was conducted using the same procedures as those described for the herbivorous diet. For each trial in the thermal gradient, two animals, each fed either a 50% or 150% ration, were tested simultaneously in each half of the gradient for four consecutive diel cycles.

Data analyses.—A general linear model repeated-measures analysis of variance (SuperAnova, Abacus Concepts, Berkely, CA) was performed with selected body temperature (T_{sel}) as the dependent variable. Five independent categorical variables were included in the model: (1) day versus night; (2) ration (50% vs 150% daily energetic need); (3) diet (herbivorous vs carnivorous); (4) day (each of the four 24-h periods); and (5) each individual lizard. The last variable was included to separate the effect of differences in responses of individual lizards from the effects of the treatments on those lizards. Selected body temperatures were averaged into mean values, for daytime and for nighttime, and for each lizard over each of three 24-h experimental periods (excluding the first 24 h, which were considered a period of acclimation to the thermal gradient).

TABLE 1. RESULTS OF A REPEATED-MEASURES ANOVA WITH MEAN SELECTED BODY TEMPERATURE (T_{SEL}; AVERAGED OVER THREE DAYS) AS THE DEPENDENT VARIABLE. Overall, lizards selected higher temperatures during the day than they did at night. Lizards fed the herbivorous diet selected higher temperatures than they did when fed the carnivorous diet. Differences in T_{sel} based on diet, however, depended upon ration (i.e., the diet × ration interaction was also significant). Individual lizards selected significantly different temperatures, and there was no significant effect of ration.

Source	df	SS	*F*-value	*P*-value
Lizards	5	80.73	2.44	0.0375
Diet	1	50.61	10.69	0.0024
Ration	1	5.26	1.11	0.2989
Diet × ration	1	44.94	9.50	0.0039
Day/night	1	80.26	16.96	0.0002
Residual	15	170.38		

RESULTS

There was a highly significant difference between T_{sel} of Desert Iguanas fed herbivorous and carnivorous diets (Table 1). Lizards underfed the herbivorous diet selected mean body temperatures 3.6 C higher than those selected by lizards underfed the carnivorous diet (Fig. 1). When lizards were fed 150% of their energetic needs, however, there was no significant difference in T_{sel} between the two diet treatments ($F_{1,14}$ = 1.05, P = 0.32; Fig. 1). The difference in T_{sel} between lizards fed herbivorous and carnivorous diets, therefore, was influenced by ration and driven by the significant interaction between diet and ration (Table 1, Fig. 1). In particular, lizards fed a reduced ration (50%) of the carnivorous diet selected significantly

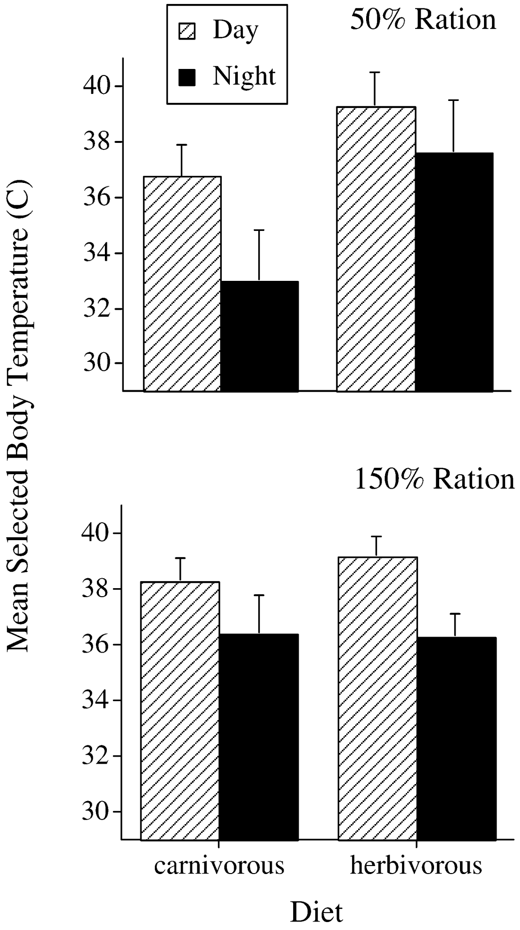

Fig. 2. Interaction plot between diet and ration. Error bars are 95% confidence limits. Lizards fed a 50% ration of the carnivorous diet selected a significantly lower mean temperature (34.9 C) than lizards underfed the herbivorous diet (38.5 C) and both well-fed treatment groups (37.3 C for canivorous diet and 37.7 C for herbivorous diet).

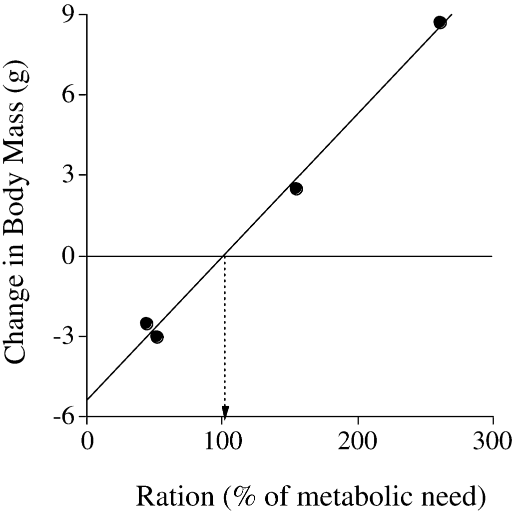

Fig. 3. Mean change in measured body mass as a function of food intake. Values are given as a percentage of daily metabolic costs, which were estimated from Equation 1 (Appendix 1). Interpolation indicates that animals will not change body mass when consuming approximately 100% of their daily energetic need (r^2 = 0.99).

lower body temperatures than did lizards in all other treatment groups (Fig. 1).

Overall, Desert Iguanas selected higher body temperatures during the day than they did at night (Table 1, Fig. 2). Lizards fed the herbivorous diet on a ration of 50% of their daily energy requirement selected warmer temperatures and had a smaller difference between daytime and nighttime body temperatures, than did the same lizards when fed the carnivorous diet on a 50% ration. When lizards were fed 150% of their daily energy needs, however, they selected similar body temperatures regardless of diet quality (Fig. 2). When fed the carnivorous diet, Desert Iguanas consuming only 50% of their daily energy needs selected lower body temperatures than did lizards fed 150% of their energy needs; and when fed the herbivorous diet, lizards thermoregulated at relatively high temperatures regardless of ration (Fig. 2).

At night, lizards fed the 50% ration of the carnivorous diet selected significantly lower body temperatures than did lizards in all other treatments ($F_{9,15}$ = 6.53, P = 0.015). During the day, however, selected temperatures of lizards across all four treatments were not significantly different ($F_{9,15}$ = 1.35, P = 0.30).

DISCUSSION

Ration and diet interactively affected thermoregulatory behavior. Desert Iguanas fed a submaintenance carnivorous diet selected significantly lower temperatures than those selected in all other treatment groups (Figs. 1, 2). This result is consistent with studies of a naturally carnivorous lizard, *Crotaphytus collaris* (Barnes, 1989; Sievert, 1989), and may be explained by the advantage of voluntary hypothermia as a means of conserving energy during quiescent periods (Regal, 1967; Barnes, 1989). For Desert Iguanas fed an herbivorous diet, however, the thermoregulatory pattern was different. These lizards selected higher body temperatures than they did on carnivorous diets regardless of ration (Figs. 1, 2). Our data, and information on the difficulty of digesting plant material (Zimmerman and Tracy, 1989), suggest that herbivorous lizards do not (indeed, may not be able to) employ voluntary hypothermia as part of a thermoregulatory approach to achieve or maintain energy balance.

Herbivorous lizards, such as Desert Iguanas, Chuckwallas (*Sauromalus obesus*) and Green Iguanas (*Iguana iguana*), may require more time at elevated body temperatures to digest refractory components (e.g., cell wall) of plant material (Troyer, 1987; Zimmerman and Tracy, 1989; van Marken Lichtenbelt, 1992). For example, neither Desert Iguanas nor Chuckwallas are able to digest plant foods if their body temperatures fall below 27 or 28 C, respectively (Harlow et al., 1976; Zimmerman, 1989). Moreover, when available, both of these species select high body temperatures at night when digesting herbivorous diets (this study; Case, 1976; Muchlinski et al., 1990; Nussear et al., 1998). For Desert Iguanas, as with other herbivorous reptiles, maintaining high body temperatures may be required to sustain gut microsymbionts (Schall and Dearing, 1994; King, 1996; Nussear et al., 1998) that aid in digesting plant cell walls (Troyer, 1991; Bjorndal, 1997). Additionally, high body temperatures might be required to prevent impaction associated with the intake of nonstructural digestibility reducers (potentially toxic compounds) found in plants eaten by some herbivorous lizards (Swift, 1987; Schall and Ressel, 1991).

High body temperatures are attainable by Desert Iguanas during much of the activity season, which generally extends from March to October (Norris, 1953). Desert Iguanas stay in burrows at night (Norris, 1953), and body temperature equilibrates with burrow temperature (Moberly, 1963). Burrow temperatures during midsummer are approximately 39 C (see DeWitt, 1963, in Minnich, 1970). Earlier and later in the activity season, burrow temperatures are cooler, ranging from the low-mid 30s C (McGinnis and Dickson, 1967; Mautz and Nagy, 1987). Thus, nighttime temperature selection may be constrained at the onset and end of the activity season, but temperatures matching those selected by Desert Iguanas in this study (Fig. 2) are available during much of the activity season.

Temperature selection during the day and night is likely determined by many interacting factors in natural habitats. Body temperatures of some reptiles are known to depend upon nutritional status, but altering body temperature selection in response to feeding, or following periods of inanition, is not universal (e.g., Gatten, 1974; Lang, 1979; Touzeau and Sievert, 1993). Daytime body temperature selection and thermoregulatory behavior of Chuckwallas in the laboratory appear to be unaffected by long periods of food deprivation (Case, 1976) or differences in food quality (Nussear et al., 1998). Chuckwallas in nature, however, abandon daytime activity and apparent thermoregulatory behaviors when confronted with an absence of succulent foods in low rainfall years (Nagy, 1973), as do Desert Iguanas (Mautz and Nagy, 1987). A less parsimonious conclusion (suggested by a reviewer) that can be drawn from these data is that lizards on a carnivorous diet have certain isozymes activated for digestion only at cooler temperatures. These isozymes might be employed when lizards have low food rations to extract needed energy from food at low temperatures.

The patterns of thermoregulatory behavior reported here could stem from factors other than energetic need, such as hydroregulation or gut fill. In particular, Desert Iguanas underfed the carnivorous diet might select lower temperatures than those in the other treatment groups because these lizards were not given as much water to balance water losses. Although both diets in our study contained 80% water, the carnivorous diet was more energy dense and, therefore, contained less water per unit of energy. Thus, lizards fed the carnivorous diet received less water than did the same lizards fed the herbivorous diet. In a laboratory study of Desert Iguanas dehydrated to 80% of their fully hydrated mass, however, neither the upper nor the lower thresholds for T_{sel} were affected by hydration level (Dupré and Crawford, 1985). Regarding gut fill, lizards fed the smallest ration of food (50% carnivorous diet) selected significantly lower temperatures than did those in the other diet/ration groups (Figs. 1, 2), suggesting that gut fill may have influenced temperature selection. Differences in the amount of food fed to individuals in the other diet/ration groups, however, were not reflected in patterns of temperature selection. Thus, although separating the mechanisms underpinning the thermoregulatory patterns reported here will require more data, the energetic hypothesis seems the best supported by the available evidence.

Time between testing animals on herbivorous and carnivorous diets may have been a factor in our results, as in studies of temporal effects on body temperature selection by lizards (e.g., Patterson and Davies, 1977; Firth and Belan, 1998; but see McGinnis, 1966; Licht, 1968). Mean temperature selected at night by lizards underfed the carnivorous diet, however, was the only temperature that differed from those selected at night by lizards in the other treatment groups

(Fig. 2). During the day, none of the mean selected temperatures differed among treatment groups. These findings suggest that differences in the diet/ration treatments, rather than seasonal/temporal differences, drove differences in body temperature selection.

Collectively, our data, and additional evidence showing that digesting plants is difficult for reptiles (reviewed in Zimmerman and Tracy, 1989; King, 1996), suggest that herbivorous lizards do not employ voluntary hypothermia as part of their thermal/energetic strategies. This hypothesis predicts that herbivorous lizards might require environments in which nighttime conditions do not force low body temperatures. Indeed, the present-day distribution of herbivorous reptiles in tropical, subtropical, and hot desert environments (Zimmerman and Tracy, 1989; King, 1996; Espinoza and Tracy, 1997) further supports this assertion.

Herbivorous reptiles are energetically less efficient than carnivores in several ways. The food eaten by herbivores is less energy dense and it is digested less efficiently. In addition, if herbivores maintain high body temperatures needed for digestion and do not undergo voluntary hypothermia in response to energetic constraints, their ability to attain energy balance through thermal reduction of metabolic rate is limited. Metabolic rate would be lower for lizards selecting cooler temperatures at night (those underfed the carnivorous diet in this study) than for lizards selecting warmer nighttime temperatures (well-fed animals on the carnivorous diet or herbivores fed either ration in this study). Higher rate of digestion at higher body temperature, however, could offset energetic costs of elevated metabolic rate. Herbivores may further attain energy balance by reducing other avenues of energy allocation such as daily activity. Clearly, hypotheses tested and generated in this study need to be addressed in other herbivorous reptiles, in both lab and field settings, to determine the generality of these potential energetic constraints for herbivorous reptiles.

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APPENDIX 1

Estimated daily energetic need for each lizard was calculated using the method of Zimmerman (1989) by taking the sum of the estimated daytime (12 h) and nighttime (12 h) energetic costs of activity (Nagy, 1977; Nagy et al., 1984), digestion (Benedict, 1932; Roberts, 1968; Gatten, 1980), and basal rates of metabolism (Andrews and Pough, 1985). Resting metabolic rate (RMR) expresses basal metabolism of an ectotherm during the day, and standard metabolic rate expresses basal metabolism of an ectotherm at night. $RMR = 0.013\ (m)^{0.8} \times 10^{0.038\ (T)} \times 10^{0.14}$, $SMR = 0.013\ (m)^{0.8} \times 10^{0.038\ (T)}$, where m = body mass (g), T = modal body temperature (C), and units = ml O_2/h (Andrews and Pough, 1985). Temperatures of 39 C during the day and 28 C at night were based on those reported by DeWitt (1967) and Brattstrom (1965) for *Dipsosaurus dorsalis.*

$$\begin{aligned}&\text{daily energetic need}\\&\quad = 0.5(\text{RMR} + \text{activity} + \text{digestion})\\&\qquad + 0.5(\text{SMR} + \text{digestion}) \qquad (1)\end{aligned}$$

We estimated activity as 2RMR (after Nagy, 1977; Nagy et al., 1984) and digestion as 0.5RMR (after Benedict, 1932; Roberts, 1968; Gatten, 1980).

The balance of energy costs and gains can be determined, according to the conservation of mass principle, by changes in mass of the animals. Thus, lizards fed more food than required to balance energetic costs will gain body mass, and those receiving less will lose mass. Interpretation of data for lizards fed different amounts of experimental foods supports the efficacy of Equation 1 for calculating energetic costs. Specifically, it is estimated that animals receiving 100% of their daily energetic need will neither gain nor lose body mass (Fig. 3).