

APPLICATION OF ALLOMETRIC FIELD METABOLIC RATE EQUATIONS TO PREDICT ENERGY AND FOOD REQUIREMENTS OF LEOPARD TORTOISES (*GEOCHELONE PARDALIS*)

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Abstract

In the absence of species specific energy requirements, allometric formulas are one method to predict practical diet quantities. The objective of this study was to quantify individual voluntary dry matter (DMI), metabolizable energy (MEI) intake and body weight (BW) in 18 juvenile leopard tortoises (*Geochelone pardalis*). Over two 15-day periods (A, B), each animal was offered a nutritionally complete, extruded tortoise diet and coastal bermudagrass hay in excess of predicted dietary energy requirements as calculated by the allometric field metabolic rate (FMR) equation ($0.232 \times \text{BW}_g^{0.813}$) for herbivorous reptiles. Environmental conditions within the animal areas were monitored. Average daily food intake, expressed in DM g or kJ ME $\text{BW}_g^{0.813-1}$, did not differ significantly between the two trials ($P > 0.05$). The average MEI of animals in this study, across both periods, was $0.162 \text{ kJ BW}_g^{0.813-1}$, or approximately 70% of the predicted MEI for herbivorous reptiles. As anticipated due to seasonal changes and open-style design of the holding area, mean ambient and floor temperatures from Period A to Period B ($P < 0.05$). Supplemental heat source temperatures did not differ significantly ($P < 0.539$). Mean BW increased with Periods A and B $16.1 \pm 41.4 \text{ g}$ ($P > 0.05$) and $29.0 \pm 50.1 \text{ g}$ ($P > 0.05$), respectively. Across the two trial periods (77 d), there was a 135.7 g increase in mean BW ($P < 0.05$). The allometric formula developed for herbivorous reptiles over-predicted the MEI of the animals in this study. Continued, long-term data collection from this controlled population of leopard tortoises should provide practical benchmarks for management of the species.

Introduction

A fundamental challenge in applied animal nutrition is determining the appropriate food quantities to offer in relation to an animal's caloric and nutrient requirements. Inappropriate quantities of food are not only potentially detrimental to animal health (e.g., malnutrition, obesity), but may have management, vector-related and financial implications.

In the absence of information regarding food intake and caloric requirements of a given species, nutritionists employ variable methods to develop practical diets. These may include: application of generalized allometric equations developed from controlled studies with a broad group of related species, utilization of a specific equation to predict energy requirements for a similar species, or determination of quantities through continued application, review and evaluation.

In a review of free-ranging animal energetics, Nagy et al. summarized field metabolic rate (FMR) data generated using the doubly-labeled water (DLW) technique from 55 reptile species.⁵ Allometric formulas were developed for all reptiles, and specifically herbivorous reptiles (Table

1). Only one tortoise, the desert tortoise (*Gopherus agassizii*), was included within the data summarized (Table 1).

Desert tortoises, native to the Mojave and Sonoran deserts of North America, consume a range of forages that vary in abundance seasonally and in relation to rainfall.^{1,2,7} Seasonally, this species hibernates in burrows. Field metabolic rates measured for desert tortoises fell below the 95% confidence interval of the generalized reptile equation, indicating that they would have field metabolic rates significantly lower than lizards of similar body mass.⁵

The objective of this study was to quantify individual voluntary food intake in leopard tortoises when offered food quantities in excess of predicted dietary energy requirements as calculated by the allometric FMR equation for herbivorous reptiles.

Methods

Animals

Eighteen, five year-old leopard tortoises (*Geochelone pardalis*), hatched at the Department of Herpetology, Smithsonian National Zoological Park and transferred to the Animal Science Department, California Polytechnic State University (San Luis Obispo, CA) were included in this study. Tortoises were randomly assigned to enclosure and housed individually. All individuals had approximately 4 months to adapt to their environment before testing.

Use of the animals indicated in this study, protocol #903, has been reviewed and approved by the California Polytechnic State University Institutional Animal Care and Use Committee.

Husbandry

All animals were housed in an open-air building enclosed on three sides. The southern exposure of the building is separated only by wire mesh to the outside environment. Within the building are six identical adjacent pens with concrete floors and walls (Figure 1). Each pen is subdivided into three enclosures of equal size (3.66 x 0.91 m) by a solid barrier (15.24 cm). Each enclosure contains a 61 x 122 cm heat pad (Stanfield[®] S2B4; Osborne Industries, 120 North Industrial Avenue, Osborne KS 67473) maintained within 25-35°C with a manual power control (Stanfield[®] F911; Osborne Industries, 120 North Industrial Avenue, Osborne KS 67473), water and food dishes (15 cm diameter) and a 30 x 36 x 24 cm three-sided box placed on top of the heat-pad.

Enclosure orientation inside the building offers a temperature gradient across which animals may pass through based on individual preference. Temperature readings, including shaded floor temperature, heat-pad surface temperature and interior building air minimum/maximum temperature, were recorded twice daily. Surface temperatures were recorded with an infrared noncontact thermometer (Raytek[®] Minitemp MT4, Raytek Corporation, 1201 Shaffer Road, Santa Cruz CA 95061).

Diet

Two identical 15 day trials were conducted: 10-24 February (Period A) and 14-28 April, 2009 (Period B). Each animal was weighed to 0.1 g in the morning on day 1, 8 and 15 of each trial. Quantities of a nutritionally complete, extruded tortoise diet (Mazuri® Tortoise Diet [5M21], PMI Nutrition International, P.O. Box 66812, Saint Louis, MO 63166-6812) equivalent to 110% of the herbivorous reptile FMR (kJ ME d⁻¹) were offered based on the following:

$$(0.232 \times BW_g^{0.813}) \times 1.1$$

where BW_g is the individual's body weight on the first day of the trial week (i.e., day 1 or day 8).⁵

The test diet contained 12.13 kJ ME g⁻¹ (PMI Nutrition International, 2009). Quantities weighed to 0.1 g sufficient to provide 110% each individual's weekly calculated caloric requirement were distributed equally over three feedings each week (e.g., day 1, 3, 5). To facilitate consumption, each animal's weighed diet was soaked with approximately 200-250 mL of water for 30 sec and drained before feeding.

On days when the test diet was not fed, 5 g of chopped (< 3/4" length) coastal bermudagrass hay (*Cynodon dactylon*) was offered. Hay was offered in the same feed bowl as the extruded diet, but was not soaked as described. This food item was offered in addition to the energy required to satisfy 110% FMR, as an occupational food.

All food was offered between 0900-1100 hours and removed between 1700-1900 hours daily. Orts were collected in labeled plastic reclosable bags. Representative samples of the test diet were collected for moisture analysis. Moisture was evaporated from the samples by drying at 50°C in an incubator (Isotemp®, Model 630D, Fisher Scientific, 2000 Park Lane Drive, Pittsburgh, PA 15275) to a constant weight. Dry matter was determined gravimetrically as the residue remaining after drying.

Statistical analysis

All pair-wise comparisons between periods were analyzed with a one-sided paired student T-test (Minitab 15; Minitab, Inc., State College, PA). Body weights for all individuals between periods were analyzed using a general linear model (Minitab 15; Minitab, Inc., State College, PA). For all statistical analyses, significance was set at $P < 0.05$.

Results and Discussion

Environment

Environmental temperatures documented across both trials are summarized in Table 2. Mean temperature of the shaded concrete floor increased from Period A to Period B ($P < 0.005$). Maximum ($P < 0.005$) and minimum ambient temperatures also increased between the two periods ($P < 0.05$). These differences were anticipated due to the climatic season and open-style design of the holding area.

The heat-pad temperatures between the two trials did not differ significantly ($P < 0.539$) (Table 1). The consistency of temperature from this source was reassuring and should be expected, based on the nature of the equipment. However, it is advisable to monitor such sources as part of daily management to minimize the potential for under- or over-heating.

The mean Period A ambient maximum and minimum, Period A floor, and Period B minimum are outside the suggested temperature range for maintenance of the species.⁴ However, the microclimate created by the supplemental heat source offered the animals a consistent region of warmth within their enclosure that could be utilized when ambient temperatures were below those preferred by an individual. A future evaluation of space utilization in relation to environmental temperature should be considered.

Intake

Tortoises did not consume coastal bermudagrass hay when offered. This observation may be in relation to the quantity extruded tortoise diet offered, rather than the bermudagrass alone. During both periods, the tortoises were offered quantities of food in excess of their projected caloric requirement, in order to quantify self regulated food intake. This presented the animals with the opportunity to select the preferred extruded tortoise diet over other coastal bermudagrass without the potential for caloric deficit. This is not unlike most practical zoo diets, where animals are offered foods in excess of caloric needs, and thus are afforded the opportunity to select preferred foods, sometimes to their nutritional detriment.

The preference for the manufactured, extruded tortoise diet in relation to coastal bermudagrass and plant foods consumed by leopard tortoises in their endemic range should be tested under more controlled conditions in the future. All further discussion of food intake is related to the nutritionally complete, extruded tortoise diet.

Average daily food intake, expressed in g dry matter (DM) or kJ ME $BW_g^{0.813-1}$, did not differ significantly between the two trials ($P > 0.05$) (Table 3). The herbivorous reptile FMR allometric equation predicts a metabolizable energy intake (MEI) of $0.232 \text{ kJ } BW_g^{0.813-1}$ to support metabolic requirements. The average MEI of animals in this study, across both periods, was $0.162 \text{ kJ } BW_g^{0.813-1}$, or approximately 70% of the predicted MEI for herbivorous reptiles. Compared to the FMR documented for desert tortoises, the tortoises in this study consumed 47.7% greater MEI than predicted.⁵

Low FMR is described as an adaptation of desert tortoises to tolerate long periods of chronic energy shortage during drought.⁷ Also observed in desert tortoises, is the plasticity of FMR, with changes observed in relation to resource (e.g., food, water) availability.² Although leopard tortoises in the southern portion of the species range are reported to experience a period of dormancy, they may not experience the same environmental pressures as the desert tortoise.³ If the level of intake observed in this study is an indication of a relatively higher metabolic rate in the leopard tortoise, these findings would be consistent with this comparison of the two species.

Body weight

Average increase in body weight from d 1 to 15 of the Period A and Period B trials was 16.1 ± 41.4 g ($P > 0.05$) and 29.0 ± 50.1 g ($P > 0.05$), respectively. Across the two trial periods (77 d), there was a 135.7 g increase in mean body weight ($P < 0.05$) (Figure 2).

It has been suggested that ‘very high, yet not desirable, growth rates are typical’ of juvenile tortoises reared using ‘scientifically formulated’ tortoise diets.³ Such statements are rarely supported with objective information that quantifies diets, nutrient intake, growth rates or sizes of specimens anecdotally determined to be ‘normal’ or ‘abnormal’. There are multiple nutrition-related factors that can influence growth, including, but not limited to diet nutrient and energy content, and quantities of diet consumed. A range of foods can be safely offered, when presented in appropriate quantities in relation to an animal’s caloric and nutrient requirements.

Although it is commonly accepted that accelerated growth can be detrimental, particularly with herbivorous tortoises, the availability of typical growth data from wild leopard tortoises monitored over time or captive bred animals maintained in controlled, environments is lacking. In the absence of such basic information, the definition of ‘normal’ open to individual interpretation. It is our hope that long-term management of this herd of leopard tortoises under closely monitored conditions will generate valuable information to promote the science-based management of the species.

Conclusions

1. When applied to the leopard tortoises included in this study, the allometric formulas developed for herbivorous reptiles and desert tortoises appear to over- and under-predict the animals’ energy requirements, respectively.
2. The partially open-air construction of the tortoise building allows the animals access to unfiltered sunlight, but at the expense seasonally variable environmental conditions.
3. Supplemental heat sources offered a consistent and reliable microclimate within each specimen’s enclosure.
4. The nutritionally complete, extruded tortoise diet was readily accepted by, and promoted positive weight gain, all specimens.
5. Baseline data generated from this controlled population of leopard tortoises should provide practical benchmarks for management of the species.

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Table 1. Summary of field metabolic rates (FMR) for selected reptiles.^{5,6}

Group	Equation	% of FMR for all reptiles
Desert tortoise	$0.1373 (BW_g)^{0.75}$	24.4
Herbivorous reptiles	$0.232 (BW_g)^{0.813}$	66.4
All reptiles	$0.196 (BW_g)^{0.889}$	100.0

Table 2. Mean (\pm SEM) maximum and minimum ambient, supplemental heat source and shaded floor temperatures ($^{\circ}$ C) within leopard tortoise enclosures during two separate measurements of food intake.

	Maximum Ambient	Minimum Ambient	Heat pad	Floor
Period A (Feb)	16.5 ± 1.23^a	8.1 ± 0.68^a	30.8 ± 0.82	15.4 ± 0.88^a
Period B (Apr)	27.0 ± 2.17^b	12.3 ± 1.57^b	30.1 ± 1.13	21.8 ± 0.95^b

^{a,b} values within column with different superscripts differ ($P < 0.05$).

Table 3. Mean (\pm SEM) intake of dry matter (DM, g) and metabolizable energy (ME, kJ) of a nutritionally complete, extruded tortoise diet offered at 110% of field metabolic rate during two separate measurements of food intake.^{1,2}

	DM, g	kJ ME
Period A (Feb)	0.013 ± 0.0007	0.15 ± 0.008
Period B (Apr)	0.014 ± 0.0006	0.17 ± 0.008

^{a,b} values within column with different superscripts differ ($P < 0.05$).

¹Field metabolic rate = $0.232 \times BW_g^{0.813}$; Intake $BW_g^{0.813-1}$

²Mazuri[®] Tortoise Diet [5M21], PMI Nutrition International, P.O. Box 66812, Saint Louis, MO 63166-6812.

Figure 1. Floor plan of Animal Science Department tortoise teaching and research facility, California Polytechnic State University, San Luis Obispo, CA.

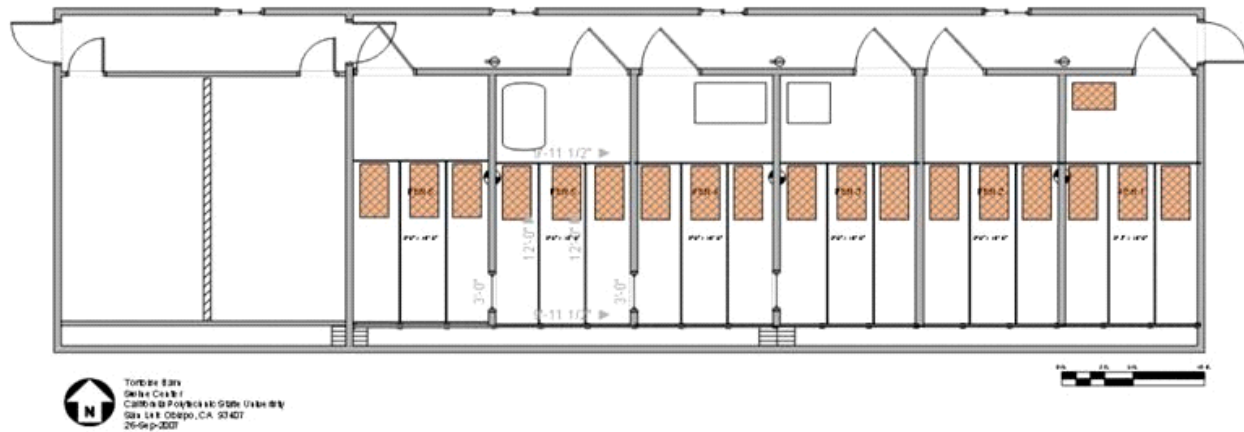


Figure 2. Mean (\pm SEM) body weight (g) of 18 leopard tortoises (*Geochelone pardalis*) offered a nutritionally complete, extruded tortoise diet at 110% of field metabolic rate (FMR) over two separate measurements of food intake; ^{a,b}columns with different superscripts differ ($P < 0.05$).

