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Is Temperature Independence of Digestive Efficiency an Experimental Artifact in Lizards? A Test Using the Common Flat Lizard (Platysaurus intermedius)

WARRICK MCKINON AND GRAHAM J. ALEXANDER

Digestive efficiency has been measured in several species of lizards and appears to be related to temperature and diet quality. We hypothesized that the apparent disagreement in the literature concerning the effect of body temperature on digestive efficiency is the result of the confounding effect of diet quality. Because high-quality diets result in very high digestive efficiencies, differences due to body temperature are proportionally small and are thus easily masked by noise. To test this hypothesis, we measured the apparent digestive efficiency in 16 common flat lizards (Platysaurus intermedius) fed a low- and high-quality diet at 31 °C and 26 °C. We standardized the quantity and controlled the quality of food ingested by force feeding the lizards using a syringe. The digestive efficiencies for the low-quality (52%) and high-quality (88%) diets were significantly different at both temperature regimes, but no significant differences were found between the digestive efficiencies measured at the different temperature regimes for either diet. Thus, our hypothesis that the degree of temperature dependence of apparent digestive efficiency is a function of food quality was falsified. This indicates that the temperature dependence of apparent digestive efficiency is a species-dependent attribute.

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DIGESTIVE efficiency (the percentage of consumed energy absorbed through the gut; Johnson and Lillywhite, 1979) is a fundamental nutritional variable that has an important effect on the energy balance of animals (Andrews and Asato, 1977). However, this measure is not known for the majority of ectothermic animals. One approach to dealing with the lack of species-specific information is to identify generalities so that the digestive efficiency measured in one species can be used in modeling the energy balance in another. At present, the effect of temperature on the digestive efficiency of lizards is not clear. In an attempt to clarify matters, we hypothesised that digestive efficiency in lizards is influenced by temperature in all cases and that reported cases of temperature independence (van Marken Lichtenbelt, 1992; Beaufre et al., 1993; Ji et al., 1993) result merely from a large noise to signal ratio (Type II error), which is especially likely when measuring high digestive efficiencies.

Digestive efficiency has been measured in a several species of lizards and, among other things, appears to be related to temperature and diet quality. In some species, digestive efficiency is clearly temperature-dependent (Harlow et al., 1976; Ruppert, 1980; Troyer, 1987), whereas in others, dependence appears to be slight (Waldschmidt et al., 1986) or even non-existent (Ruppert, 1980; Karasov and Diamond, 1985; Zimmerman and Tracy, 1989). Digestive efficiencies of lizards also appear to vary over a wide range and may be as low as 30% for some herbivorous species (Ruppert, 1980) and exceed 90% for some carnivorous or insectivorous species (Johnson and Lillywhite, 1979). High digestive efficiencies have also been measured for herbivorous species of lizard maintained under conditions where animals are able to attain selected T_b and are fed a high-quality diet (Throckmorton, 1973).

Because digestive efficiencies of lizards fed high-quality diets may exceed 90%, any differences in efficiency at different temperatures must, by definition, be small (digestive efficiency cannot exceed 100%). Thus, differences in digestive efficiency may be masked by noise (variation in the measures due to inaccuracies of technique or equipment), and this may result in any temperature dependence of digestive efficiency being hidden. We tested for this masking effect by measuring the digestive efficiency of the lizard Platysaurus intermedius, fed a high-quality and low-quality diet at two temperatures. If the signal to noise effect was indeed responsible for “apparent” temperature independence under certain feeding regimes, our expectation was that we should record a temperature dependence for the high-quality diet but not for the high-quality diet. Alternatively, temperature dependence or temperature independence for both diets indicates that the signal to noise ratio does not have an influence on the result.
Digestive efficiency is a measure of the ability of an organism to extract energy from a food substrate and is given by the following equation:

\[ \text{digestive efficiency} = \frac{C - F}{C} \times 100 \]  

(after Johnson and Lillywhite, 1979), where C is the energy value of food consumed and F is the energy value of the fecal waste. This measure is better termed “the apparent digestive efficiency” (ADE) and differs from the “true digestive efficiency” because not all excretory products produced (e.g., gut epithelium) are the immediate result of ingested food. Because it is not practical to separate these from the fecal waste, their inclusion results in a slight underestimation of digestive efficiency.

The genus *Platysaurus* (Family: Cordylidae) is a speciose genus of rupicolous (rock-living), omnivorous lizards (Whiting and Greeff, 1997; Cooper et al., 1997) endemic to the southern parts of Africa (Mouton and van Wyk, 1997). Broadley (1978) reports that *P. intermedius* is primarily insectivorous but that up to 35% of the diet may consist of vegetative material. *Platysaurus intermedius* is limited to Zimbabwe and the eastern parts of South Africa and Swaziland (Branch, 1988). Individuals reach a maximum snout–vent length of 80 mm and rarely exceed 10 g in mass. A dorsally compressed body (± 5 mm trunk thickness) allows lizards to squeeze into rock crevices and also ensures that body temperature is usually very similar to substrate temperature.

MATERIALS AND METHODS

Sixteen *P. intermedius* lizards (5.12 g ± 1.7; mean ± SD) were captured in Mpumalunga Province, South Africa (24°35′S; 31°11′E, altitude 700 m) using sticky-traps. Lizards were individually housed and acclimated to captivity in glass terraria (300 × 225 × 225 mm), each containing several rocks, for one month before experimentation. Ambient temperature during this period was constant at 28°C and animals were exposed to a L:D 12:12-photo period (local dawn 0800). During this acclimation period, lizards were fasted until no undigested material was seen in the feces (checked once per day). The time taken for animals to stop passing feces with undigested material was used as an estimate of gut passage time.

Feeding trials were arranged so that one-half of the lizards, randomly assigned, were fed a high-quality diet that consisted of a homogenized mixture of two-thirds commercial canned dog food and one-third commercial cake flour by mass. The remaining lizards were fed a lower quality feed where ground wheat husks replaced the flour to reduce overall digestibility. Lizards were force fed by inserting 0.2 ml food into the throat using a 1-ml syringe every second day for a total period of nine days. A strip of plastic film was slipped into the mouths of the lizards to facilitate the insertion of a pair of fine forceps, which in turn were used to open the mouth and allow insertion of the syringe for feeding. The initial feeding period was followed by an observed passage time of three days, during which time the lizards were fasted. Thereafter, diets were switched so that each lizard was tested for both diets. During these feeding periods, temperature remained constant at 31°C (SD 1; high end of selected thermal range; unpubl. data).

After the completion of the two feeding trials, the lizards were acclimated to an ambient temperature of 26°C for one week, during which time they were fed ad libitum on a varied diet of insects and canned dog food. The same protocol as described for the 31°C temperature regime was then followed at 26°C but with one exception; the volume of low-quality food fed to the larger lizards (> 5 g body mass) was increased from 0.2 ml to 0.3 ml per feed to prevent weight loss. [During feeding trials at 31°C, the eight largest lizards (> 5 g) fed the low-quality diet lost an average of 5.2% body mass].

Excreta produced by each lizard during each of the four feeding trials (feces with as much urinary products as possible removed) were collected and dried at 50°C to constant mass and then weighed. Energy values for excreta were analyzed for energy content using a bomb calorimeter (Digital Data Systems CP500 Calorimeter systems, Johannesburg, South Africa). Because a minimum of 0.5 g is needed for bombing (most accurate for equipment), samples of excreta produced by all the individuals in the same feeding trial were combined. We measured as many subsamples as possible (not less than five in each case) until all the excreta had been combusted.

Energy values for the food were also analyzed for energy content using a bomb calorimeter.
The energy content of the different feeds were 17.87 kJ/g dry mass (SD 0.06, n = 10) for the high quality and 18.33 kJ/g dry mass (SD 0.03, n = 10) for low quality. Wet mass per 0.2 ml feed in each diet was 0.256 g (SD 0.009, n = 10) and 0.227 g (SD 0.011, n = 10), respectively. The water content of the high- and low-quality diets was 54% and 60%, respectively. The high-quality diet was thus 9.65 kJ/ml, and the low-quality diet was 8.25 kJ/ml.

Using measures of energy content of food and feces, and measures of food consumption and fecal production, we were able to determine the ADE for each lizard for each of the four feeding trials. Because altering a diet may change the composition of an endosymbiont population (Troyer, 1984) and thus ADE, we also compared the ADE of animals tested first and second in all diet categories.

We used a two-way repeated measures ANOVA (temperature and diet as factors) to compare temperature and diet classes. An unpaired t-test was used to assess the effects that changes in the endosymbiotic population may have on ADE (i.e., to test between animals fed first or second on any particular diet).

**RESULTS**

Differences in ADE for different diet qualities were significant, but differences at different temperature regimes were not (Table 1, Fig. 1). Apparent digestive efficiency was 88% (SD 4) for the high-quality diet and 52% (SD 4) for the low-quality diet, irrespective of temperature. Our measures of passage time suggested that gut passage was six days at 26 C in comparison to three days at 31 C. There were no significant differences in ADE between lizards fed the high-quality diet first or second during trials, indicating that trial sequence had little effect on ADE measures (Table 2). Mean body mass change over the feeding periods was a gain of 1.9 g (SD 0.1).

**DISCUSSION**

We measured ADEs of 88% and 52% in *P. intermedius* for the high- and low-quality diets, respectively, in our study. We found no significant differences in ADE due to temperature for either of these food types. Because temperature independence of ADE was found even for the low-quality diet, our hypothesis that apparent temperature-independent ADE is only the result of signal to noise ratio (Type II error) is falsified. This indicates that ADE in *P. intermedius* is temperature independent over the temperature range tested, which spans the selected thermal range for this species. However, it is possible that ADE will differ significantly at temperatures well below the selected thermal range. Our rough measure of passage time indicates that the rate of digestion appears to be strongly influenced by temperature, because gut passage time doubled with a 5 C drop in temperature. Thus, *P. intermedius* appears to digest food more slowly but is able to extract energy just as efficiently at lower temperatures.

Our study highlights the importance of diet as a determinant of ADE. The difference in ADE of 36% between the two diets illustrates how a simple change in the carbohydrate digestibility can alter the percentage energy a lizard is able to extract from ingested food. Thus, comparisons of ADEs between species may only be valid if food type is controlled or standardized. Free-ranging lizards may also procure vastly different amounts of utilizable energy depending on diet, which can vary considerably.
TABLE 2. DIFFERENCES BETWEEN THE ADE (± SD) OF LIZARDS FED THE HIGH- AND LOW-QUALITY DIET IN THE FIRST AND SECOND TRIALS (n = 16). Nonsignificant differences indicate that endosymbiont populations did not affect ADE. n = 16; ns = not significant (P > 0.05).

<table>
<thead>
<tr>
<th>Trial</th>
<th>Mean ± SD ADE of animals (%)</th>
<th>Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>High temp high quality</td>
<td>90.5 ± 2.9</td>
<td>88.1 ± 2.1</td>
</tr>
<tr>
<td>High temp low quality</td>
<td>53.5 ± 4.2</td>
<td>48.0 ± 7.6</td>
</tr>
<tr>
<td>Low temp high quality</td>
<td>85.7 ± 7.0</td>
<td>87.4 ± 7.9</td>
</tr>
<tr>
<td>Low temp low quality</td>
<td>53.7 ± 5.2</td>
<td>50.7 ± 2.9</td>
</tr>
</tbody>
</table>

between seasons. Because many lizard species are generalist feeders, taking a wide variety of food items (Schoener, 1977), estimation of energy assimilation rates of free-ranging lizards is problematic but can be overcome if seasonal changes in diet are known. However, ADE measurements have been interpreted as being a species-specific attribute rather than of the diet. For example, herbivorous species are often said to have lower ADEs than carnivorous species (e.g., Pough, 1973). Our results indicate that these differences are most likely a result of the diet rather than a species-specific attribute. For example, Ruppert (1980) found that, when herbivorous lizards were fed a carnivorous diet, they increased their ADE to levels normally associated with carnivorous species.

The majority of studies that have investigated the ADE of lizards have reported a strong influence of temperature (Dutton et al., 1975; Harwood, 1979; Buffenstein and Louw, 1982). Our study found a contrasting result for P. intermedius and is in agreement with van Marken Lichtenbelt (1992) in this respect. van Marken Lichtenbelt (1992) found no clear temperature trend of ADE over a range of 29.4-34.6 C Tt in Iguana iguana. Although Ji et al. (1995) report "slight" temperature effects on assimilation efficiency, the results of their statistical analysis show otherwise (P = 0.735). Ruppert (1980) reports no influence of temperature in Sauromalus obesus but did find temperature effects in Crotophytus collaris. Because S. obesus is herbivorous and C. collaris carnivorous, Ruppert (1980) suggests that temperature-independent digestive abilities may be of value to herbivorous lizards because they consume a diet high in cellulose, and he alludes to this being the selective force resulting in the evolution of temperature-independent ADE. However, this does not explain the temperature-independent digestion efficiency of P. intermedius in our study, because this species is primarily insectivorous (Broadley, 1978). In any event, similar advantages would be accrued to carnivorous lizards having temperature-independent digestion. Snakes (which are carnivorous) that have been investigated have also shown temperature-independent ADE (Greenwald and Kanter, 1979).

We found a clear temperature effect on gut passage time, suggesting that the rate of digestion in P. intermedius is strongly influenced by temperature. This result is similar to that reported for other lizards (Waldschmidt et al., 1986; van Marken Lichtenbelt, 1992; Beaupre et al., 1993) and highlights the importance of temperature in rates of energy acquisition and energy budgets of lizards.

A potential source of error in our study was variation in gut fauna and flora with diets. The presence of endosymbiont bacteria has been implicated in digestive processes of some species of lizards (Troyer, 1984; van Marken Lichtenbelt, 1992). It is conceivable that a lizard, fed a particular diet, could undergo changes in the endosymbiont population in its gut. This could then affect subsequent ADE measures. However, we detected no such effect in our study when we tested for differences in ADEs between lizards fed the high-quality diet during the first or second trial.

We conclude from our study that ADE in P. intermedius is dependent on diet but not temperature, at least over the temperature range tested. The rate of digestion, measured using gut passage time was found to be temperature dependent and was significantly higher at 31 C, regardless of diet type.

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