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# An energy budget for the lizard Pseudocordylus melanotus melanotus, an extreme sit-and-wait forager

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ORIGINAL PAPER

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# The effect of temperature on digestive and assimilation efficiency, gut passage time and appetite in an ambush foraging lizard, *Cordylus melanotus melanotus*

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**Abstract** In ectotherms, an increase in body temperature increases metabolic rate and may increase rates of digestive processes. We measured the thermal dependence of the apparent digestive and apparent assimilation efficiencies (ADE and AAE), gut passage time (GP) and appetite in *Cordylus melanotus melanotus*, a medium sized Crag Lizard, which is endemic to South Africa. Trials were conducted at 20, 22, 25, 30, 32 and 35 °C under controlled conditions. Trials lasted 14 days, during which, lizards were fed ca. 1 g mealworms per day. Glass beads were used as markers to determine GP at the beginning and end of trials. Faeces and urates were collected daily and oven dried at 50 °C. The energy content of egested matter was then measured using bomb calorimetry. ADE and AAE were not affected by temperature for either males or females. The mean ± SE ADE and AAE were 94.4 ± 0.3% and 87.2 ± 0.6%, respectively. GP was not significantly different between males and females at any temperature, but decreased significantly with increasing temperature. Appetite was significantly different between the different temperatures measured. The decrease of gut passage time with increasing temperature was expected, since the digestive and assimilation efficiencies are similar over the range of temperatures tested. Lizards are thus assimilating a similar proportion of ingested energy, but at faster rates at higher temperatures. The results indicate that the digestive physiology of this species results in maximum energy gain per meal in environments where food is scarce.

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**Abbreviations** *AAE* apparent assimilation efficiency · *ADE* apparent digestive efficiency · *AE* assimilation efficiency · *DE* digestive efficiency · *GP* gut passage rate · *NEA* net energy absorbed through gut · *NER* net usable energy retained · *SVL* snout-vent length · $T_b$ body temperature

## Introduction

The successful ingestion of energy and the effective allocation of that energy are essential to an organism's activity, growth, reproduction, and ultimately, it's overall success (Nagy 1983; Secor 2001). Once food has been consumed, mechanical and chemical means make the products of digestion available for assimilation (Prosser and DeVillez 1991). These nutrients are then channelled either into metabolic pathways, or into storage. For an ectotherm, energy flux is significantly impacted by body temperature ($T_b$; Stevenson et al. 1985). Rates of both metabolism and digestion are temperature dependent; as $T_b$ increases or decreases, metabolism and digestion respond accordingly (Greenwald and Kanter 1979; Naulleau 1983; Lillywhite 1987). Two related components of digestion that have been found to be influenced by $T_b$ are gut passage time (GP) and efficiencies of energy acquisition.

GP is the time taken for any given meal to pass through the digestive system of an animal. Du et al. (2000) noted three patterns of the thermal dependence of GP in lizards: (1) GP decreases with increasing temperature, (2) GP decreases with increasing temperatures at low temperatures and levels out at high temperatures, and (3) GP decreases with increasing temperatures at low temperatures and increases at high temperatures. Food type may also influence GP. *Klauberina riversiana*, an omnivorous lizard, was found to have a GP that was twice as fast when maintained on a diet of mealworms

than when maintained on apple (Johnson and Lillywhite 1979).

The efficiencies of energy intake are commonly expressed as digestive efficiency (DE) and assimilation efficiency (AE). Technically, DE and AE are calculated from the measured energy content of the ingested meal, faeces and excreted nitrogenous waste. DE represents the relative percent of ingested energy that is absorbed across the gut wall, quantified as food energy minus faecal energy divided by food energy. AE represents the percent of ingested energy that is absorbed and which is available for metabolism following the subtraction of absorbed energy that is lost through excretion of nitrogenous waste (ammonia, urea and/or uric acid) and it is quantified as food energy minus faecal and excreted energy divided by food energy (see Table 1 for equations). It should, however, be noted that it is not technically possible to measure actual DE and AE because faeces include other components that did not originate from the meal (Mitchell 1964), including bacteria, sloughed intestinal cells and bilirubin. The energy content of faeces therefore overestimates the energy of undigested food such that the calculated efficiencies are inherently an underestimation of the actual DE and AE. Thus, the measured DE and AE are thus better termed the "Apparent Digestive Efficiency" (ADE) and "Apparent Assimilation Efficiency" (AAE) (McKinon and Alexander 1999).

Digestive efficiency of most lizards and snakes generally approaches or exceeds 90% (Lillywhite 1987), but may vary according to the type of food consumed (Slade et al. 1994). *Klauberina riversiana* has an ADE approximately 5% greater when fed on mealworms, than when fed on apple (Johnson and Lillywhite 1979). Bedford and Christian (2000), however, suggest that carnivorous reptiles usually have a higher efficiency than herbivores, but this difference may be due to the inability to chew thoroughly and the absence of cellulolytic intestinal microflora (Johnson and Lillywhite 1979).

Our study deals with the thermal dependence of digestive processes in the Drakensberg Crag Lizard, *Cordylus melanotus melanotus*. The objectives of our study were to investigate the effects of temperature on ADE, AAE, GP and appetite as part of a larger study on the energy budget of this species in its natural environment. Previous studies (Cooper et al. 1997; McConnachie and Whiting 2003) indicate that *C. m. melanotus* is an extreme sit and wait forager and study of the digestive physiology of this lizard is thus useful in elucidating the relationship between digestive physiology and feeding strategy. We show that $T_b$ significantly impacts GP and appetite, but has no effect on digestive efficiencies. Thus, lizards can speed up GP without any loss of energy assimilation by selecting higher $T_b$ during digestion, but can also extract energy efficiently at low $T_b$.

**Table 1** Processes, symbols and definitions used to calculate digestive and assimilation efficiencies (adapted from Johnson and Lillywhite 1979)

| Process | Symbol | Definition |
|---|---|---|
| Consumption | C | Energy consumed |
| Faeces | F | Energy of faecal waste |
| Urates | U | Energy of urinary waste |
| Egesta | F + U | Energy of both faecal and urinary wastes |
| Digestive energy | C−F | Energy absorbed through gut |
| Digestive efficiency | (C−F)/C×100 | Energy absorbed through gut (%) |
| Assimilation | C−(F + U) | Usable energy retained by the animal |
| Assimilation efficiency | (C−(F + U))/C×100 | Usable energy retained by the animal (%) |

## Materials and methods

### Study animal

The Drakensberg Crag Lizard (*C. m. melanotus*; formerly *Pseudocordylus*; Cordylidae) is a rupicolous, extreme sit-and-wait forager (Cooper et al. 1997) that is endemic to the eastern escarpment in South Africa. The lizards occur in dense colonies on rocky outcrops (Branch 1998) and are conspicuous when using rocks as perch sites (McConnachie and Whiting 2003). *Cordylus m. melanotus* are sexually dimorphic, such that males are larger and more brightly coloured than females (Mouton and van Wyk 1993). Snout-vent length (SVL) averages between 80 mm and 120 mm, but may reach a maximum of 143 mm in males (Branch 1998) and during the breeding season, males respond aggressively toward other males (Moon 2001). Although Branch (1998) records this species as being omnivorous, analysis of stomach contents of 40 preserved museum specimens revealed only invertebrate prey (S. McConnachie unpublished data).

All lizards used in our study originated from the Suikerbosrand Nature Reserve, approximately 40 km southeast of Johannesburg, South Africa (26 °27′–26 °34′S, 28 °09′–28 °21′E; 1,800 m above sea level). The habitat in this area is typically Highveld Grassland (Rutherford and Westfall 1986) with numerous rocky outcrops, especially in the higher lying parts. Rainfall is less than 500 mm per year and is summer seasonal. The climate is typically temperate; winters are cold with frequent frosts and very occasional snow, while summer temperatures frequently exceed 30 °C.

Lizards were acclimated in captivity for a minimum of 1 month before trials began. Lizard body mass increased by 15.2 ± 2.3% after approximately 6 months in captivity. Individuals of this species have previously been maintained in captivity in excess of 3 years and generally appear to adapt well to captive conditions.

### Methods

Methods used were similar to those used by Johnson and Lillywhite (1979). Twenty lizards (10 male, 10 female) were housed individually in 0.3×0.3×0.5 m glass terraria, with a shelter and water (supplied ad libitum). Lizards were maintained on a diet of mealworm larvae (*Tenebrio* sp.) in a temperature-controlled room (± 1 °C) with a light:dark cycle of 12:12 h. ADE and AAE, GP (used as an indirect measure digestive rate) and appetite were measured at 20, 22, 25, 30 32 and 35 °C. The sequence of trials was randomised. There was a minimum period of 7 days between trials during which lizards were maintained at room temperature (20–28 °C) and given unlimited amounts of food and water. We assumed that the inter-trial period removed the effects of the previous feeding trial.

During each trial, lizards were offered approximately 1 g mealworms per day for 14 days. Uneaten mealworms were collected, counted and weighed after 24 h. Gut passage time was measured by force-feeding lizards small glass beads on days 1 and 14 of each trial,

and recording the number of days taken for the beads to appear in the lizards' faeces. Blue and white beads were used at the start and end of trials, respectively, as these colours were easily visible in the faeces. Lizards were offered mealworms ad libitum after day 14 until white beads were passed. Gut passage time was taken as the number of days between consumption and defecation of the beads. Two measures of GP were taken per lizard since beads were used to indicate the start and end of trials—lizards were fed ad libitum before and after trials, therefore beads marked faeces from meals consumed between bead markers. Appetite was measured in two ways: as the total mass and as the number of mealworms consumed in the 14-day trial.

The trial at the highest temperature (35 °C) was terminated after 3 days because the lizards showed obvious signs of distress and it was evident that their appetite was considerably reduced. Data collected during this trial were used only for appetite measures and were made comparable to the data collected during the other trials by increasing measures proportionately (i.e. measures were multiplied by 4.7).

Food consumption was determined by subtracting the mass of the uneaten mealworms from the total mass of mealworms offered to each lizard. The mass of the uneaten mealworms was adjusted to compensate for weight loss that the mealworms experienced due to dehydration during trials. Since this weight loss was dependent largely on the temperature regime, we kept a sample of 10 mealworms in an empty terrarium (conditions the same, only without a lizard) during each trial and reweighed these mealworms after 24 hr to estimate rates of weight loss at each experimental temperature.

All faeces and urates egested during the feeding period (14 days) were collected and separated daily. Urates were separated because it is considered metabolic waste rather than faeces. Faeces and urates were dried in an oven at 50 °C until reaching constant mass. The faeces and urates were then milled for a minimum of 30 s in a high speed, water-cooled mill (IKA type A10; 20,000 revolutions per min) and the energetic content was measured by subjecting 0.5–0.7-g samples to bomb calorimetry (Digital Data Systems CP500 Calorimetry Systems, Johannesburg, South Africa). Energy content of mealworms was measured in the same manner. Mean ADE and AAE for each temperature were calculated for males and females using the equations in Table 1. Unfortunately, the small amounts of faeces and urates produced by the lizards necessitated pooling of samples for measurements of energy content. ADE and AAE values were used to calculate the net energy absorbed through the gut and the net usable energy retained by the animal for each temperature, respectively.

GP and appetite were compared between males and females, and among temperatures using a one-way repeated measures ANOVA. Since GP and appetite were not significantly different between the sexes, data for males and females were pooled. The effects of body mass and temperature on GP and appetite, and the effects of temperature on ADE and AAE, were investigated using regression analysis.

## Results

### Gut passage time

GP was determined by the first appearance of blue and white beads at the beginning and end of trials. Defecation of the beads was usually staggered over two droppings. There was no significant difference in GP between males and females at different temperatures ($F_{9,85} = 1.39$, $P = 0.21$). GP decreases significantly with increasing temperature ($R^2 = 0.92$, $P = 0.01$; Fig 1). Mass effects on GP were only evident at 22 °C, where larger lizards showed shorter passage times than did smaller lizards ($R^2 = 0.27$, $P = 0.02$; Fig 2), but the low $R^2$ indicates that, even though the relationship is significant, only a small fraction of variation in GP is explained by body mass.

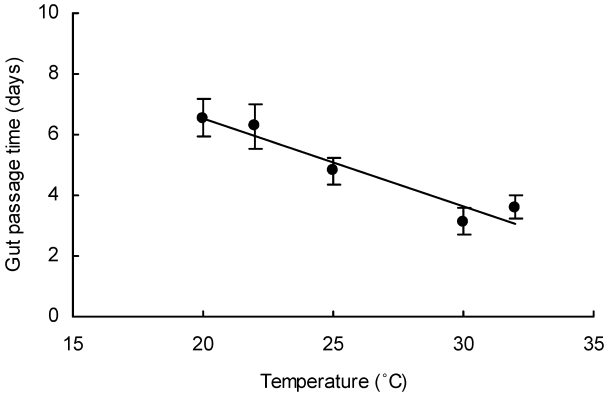



**Fig. 1** The effect of temperature on gut passage time for *Cordylus melanotus melanotus* (Mean ± SE; $N = 20$, 10 male 10 female for all temperature treatments; regression analysis; $y = -0.29x + 12.29$, $R^2 = 0.92$, $P = 0.01$)

### Appetite

There were significant differences in appetite at different temperatures, measured as either number or mass of mealworms eaten (number: $F_{9,89} = 9.52$, $P < < 0.001$; mass: $F_{9,89} = 9.15$, $P < < 0.001$). Regression analysis revealed that both number and mass of mealworms eaten increases significantly with increasing temperature (number: $R^2 = 0.91$, $P = 0.01$; mass: $R^2 = 0.89$, $P = 0.02$; Fig 3). Lizard body mass effects were evident for both number and mass of mealworms at 25 °C, where larger lizards ate proportionally more than smaller lizards ($R^2 = 0.27$, $P = 0.02$, Fig 4). The low $R^2$ value, however, suggests that although significant, the effect of body mass is small.

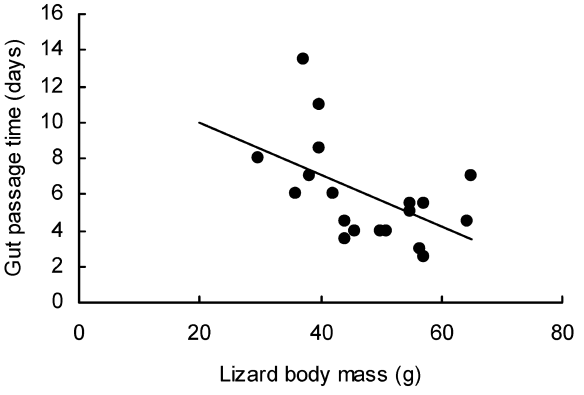



**Fig. 2** The effect of body mass on gut passage time for *C. m. melanotus* at 22 °C ($N = 20$, 10 male 10 female; regression analysis; $y = -0.14x + 12.79$, $R^2 = 0.27$, $P = 0.02$). This was the only trial where body mass had a significant effect on gut passage time

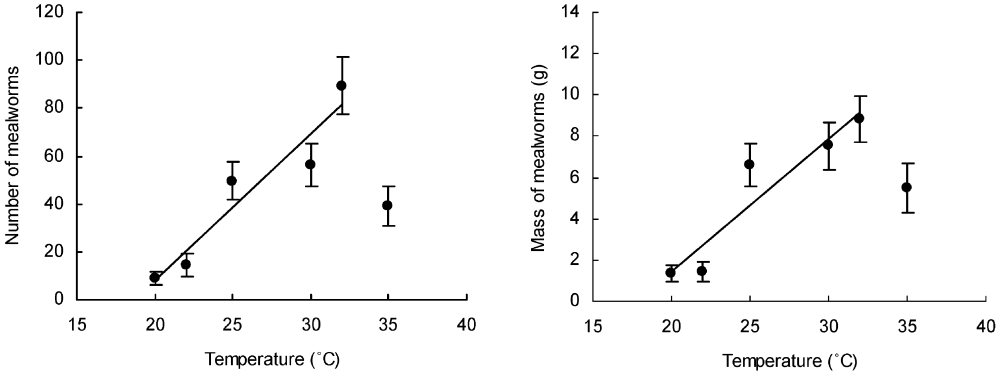



**Fig. 3** The effect of temperature on appetite in terms of the number of mealworms eaten (*left*), and of temperature on the mass of mealworms eaten (*right*) for *C. m. melanotus* (regression analysis; number: $y = 6.15x - 114.86$, $R^2 = 0.91$, $P = 0.01$; mass: $y = 0.65x - 11.55$, $R^2 = 0.89$, $P = 0.02$; Mean ± SE; $N = 20$, 10 male 10 female for all temperature treatments). Measurements at 35 °C were not included in the regression analysis because lizards showed distress and the trial was aborted after only 3 days

### Digestive and assimilation efficiency

The mean (±SE) energy contents, per gram dry mass, for mealworms, faeces and urates were 24.8 ± 0.05 kJ/g, 15.2 ± 0.20 kJ/g and 10.7 ± 0.04 kJ/g, respectively. We found no significant effect of temperature on either ADE or AAE (ADE: $R^2 = 0.05$, $P = 0.72$; AAE: $R^2 = 0.18$, $P = 0.48$; Fig 5). For these lizards consuming mealworms, ADE averaged 94.4 ± 0.3% and AAE averaged 87.2 ± 0.6%.

### Net energy gain

Both net energy absorbed (NEA) and net energy retained (NER) increased significantly with increasing temperature (NEA: $R^2 = 0.89$, $P = 0.02$; NER: $R^2 = 0.90$, $P = 0.01$; Fig 6). This was expected because an increase in energy gain with increasing temperature is simply a function of lizards eating more at higher temperatures, since neither AAE nor ADE were affected by temperature.

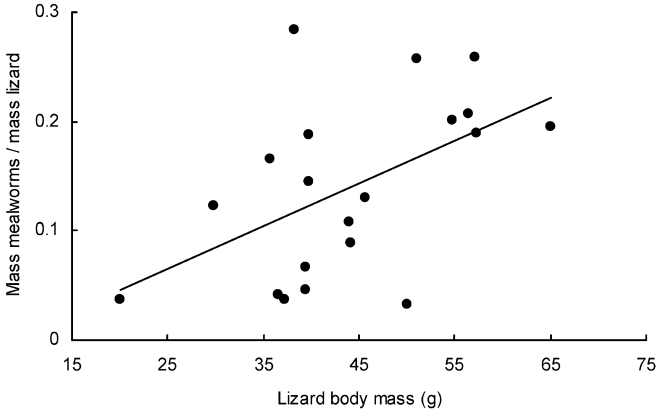



**Fig. 4** The effect of body mass on food consumption (proportional to lizard body mass) at 25 °C (regression analysis; $y = 0.004x - 0.03$, $R^2 = 0.27$, $P = 0.02$; $N = 20$, 10 male 10 female). This was the only trial where body mass had a significant effect on food consumption

## Discussion

Our study revealed that the digestive physiology of *C. m. melanotus* is highly temperature dependent in certain respects (i.e. rate of digestion and appetite), but is remarkably temperature independent in other respects (the general efficiency of energy extraction from a meal). We found that GP decreased with increasing temperature and was generally not affected by lizard body mass (only one exception where there was a small mass effect at 22 °C, where larger lizards had a marginally shorter GP). Neither ADE nor AAE were affected by temperature over the temperature range tested. Appetite increased significantly and dramatically with increasing temperature, although data collected during the first 3 days of an aborted trial at 35 °C indicates that appetite is also suppressed at high temperatures. We detected a small body mass effect on appetite for the 25 °C trial only, where larger lizards consumed a relatively larger amount of food. The thermal dependency of gut throughput rate results in the net energy absorbed through the gut and net usable energy retained also increasing with temperature under conditions where food availability is not limiting.

### Passage rate and appetite

The reduction in GP, or increased digestive rate at higher temperatures, follows the pattern typical for most reptiles (Greenwald and Kanter 1979), and has been reported for the lizards *Lacerta vivipara* (Van Damme et al. 1991), *Sceloporus merriami* (Beaupre et al. 1993), *Eumeces elegans* (Du et al. 2000), *Platysaurus intermedius wilhelmi* (Alexander et al. 2001), and the snakes *Elaphe guttata* (Greenwald and Kanter 1979), *Vipera aspis* (Naulleau 1983) and various Australian pythons (Bedford and Christian 2000). The shorter passage time may also contribute to the improved appetites at higher temperatures (Angilletta 2001), as the higher throughput at higher temperatures simply allows for more food to be

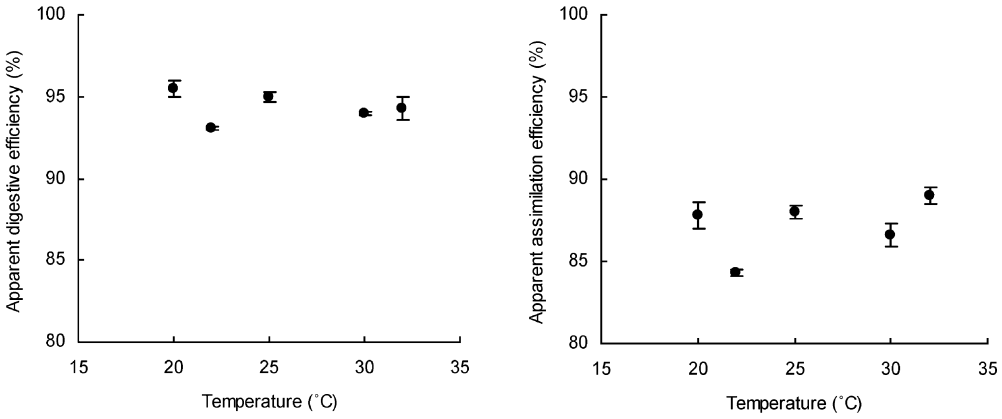



**Fig. 5** The effect of temperature on apparent digestive efficiency (*left*), and of temperature on apparent assimilation efficiency (*right*) for *C. m. melanotus* (Mean ± SE, $N = 20$, 10 male 10 female for all temperature treatments)

processed. Passage time could thus be the proximal limiting factor of consumption at low temperatures (Angilletta 2001) and could affect consumption directly through appetite modulation under conditions where food availability is not limiting. However, field measures for *C. m. melanotus* indicate low rates of ingestion (McConnachie and Whiting 2003) and suggest that food availability, rather than appetite, is likely to be the most important limitation on consumption under natural conditions.

The decrease in gut passage time with increasing temperature may explain the temperature independence of ADE and AAE in *C. m. melanotus*. At lower temperatures, digestion and absorption occurs at slower rates, and the passage of the meal is at a pace that matches its digestion and absorption. Thus, slower rates of extraction are compensated for by slower throughput, enabling the lizards to fully digest their meals at low temperatures. This digestive compensation at low temperatures is similar to digestive compensation to low food quality as reported by Hume (1989) for herbivores eating poor quality forage, and are also in agreement with the findings of Wang et al. (2003) and Secor and Faulkner (2002) of the temperature independence of specific dynamic action.

Naulleau (1983) predicted that digestion would actually cease altogether at extreme temperatures, but that food would still be passed in order to prevent putrification in the gut. However, digestion at these extreme temperatures is not usually tested in most studies since appetite is greatly reduced at extreme temperatures and there are thus practical problems of inducing the animals to feed. Even so, the increased passage time at higher temperatures that has been reported in some studies supports the hypothesis. In the lizard *E. elegans*, passage time decreases with increasing temperature but then increases above 34 °C (Du et al. 2000). Stevenson et al. (1985) noted that, in *T. e. vagrans*, passage time decreased, levelled, and then increased at 35 °C. In our study, the reduced appetite during the aborted 35 °C trial, suggests that passage time might also be decreased at this 'extreme' temperature. Further evidence also comes from the observation that some of the lizards in the 35 °C trial passed almost complete, undigested mealworms or regurgitated mealworms whole.

Various methods have been used to measure gut passage time, the most simple of which is fasting before trials (Alexander et al. 2001), where the first appearance of faeces after starvation indicates the gut passage time. This is, however, not always a suitable method. A down-regulation of metabolic physiology may occur while fasting (Secor and Diamond 2000) and once the animal is fed, it may take longer to pass through the gut because of extra time taken for up-regulation before digestion can begin. However, a number of recent studies (Starck and Beese 2001, 2002; Overgaard et al. 2002; Holmberg

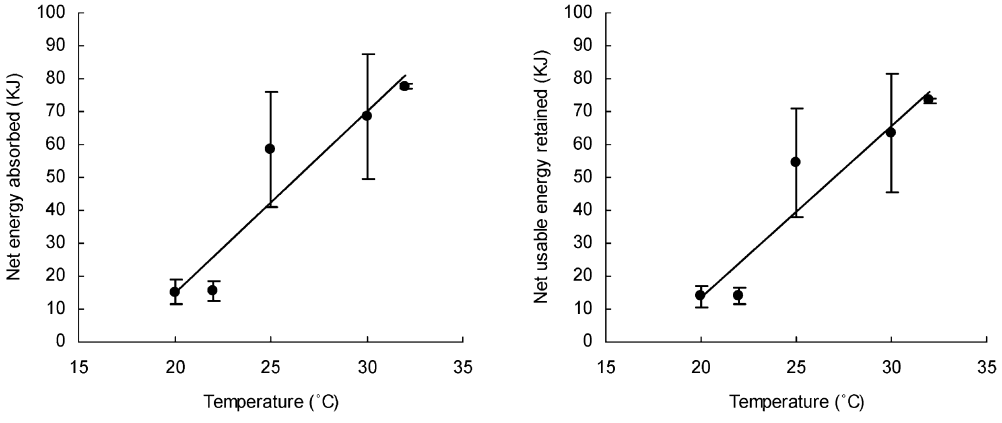



**Fig. 6** The effect of temperature on the net energy absorbed through the gut (calculated from apparent digestive efficiency; *left*), and of temperature on the net usable energy retained (calculated from apparent assimilation efficiency; *right*) for *C. m. melanotus* (regression analysis; NEA: $y = 5.50x - 94.70$, $R^2 = 0.89$, $P = 0.02$; NER: $y = 5.19x - 90.02$, $R^2 = 0.90$, $P = 0.01$; Mean ± SE; $N = 20$, 10 male 10 female for all temperature treatments)

et al. 2003) indicate that the reptilian gut may not be as down-regulated during fasting as originally proposed by Secor and Diamond (e.g. 1995, 2000). There is a distinct possibility that *C. m. melanotus* is a down regulator since observations of free-ranging individuals suggest that it is an infrequent feeder; McConnachie and Whiting (2003) reported only two attempts at prey capture in 795 min focal animal analysis. Cooper et al. (1997) also report ambush foraging to be the typical mode of foraging in this clade (formerly *Pseudocordylus*). Thus, fasting before trials would certainly be an inappropriate method for measuring GP in *Cordylus* since the gut of a fasted lizard may require some start-up time.

Dyes, such as powdered fluorescent dyes, have also been used as markers, with or without small, indigestible objects such as short pieces of fishing gut (Waldschmidt 1986; Beaupre et al. 1993). The dye is usually introduced into the food and, in the case of insect prey, it is injected through the exoskeleton of the insect before it is offered as food (e.g. Beaupre et al. 1993). However, the use of dyes was not practical in our study, since this would have necessitated the injection of dye into 250 mealworms per day at the start and termination of each trial. Also, the rupture of the mealworms' exoskeleton resulting from administering the dye would likely have changed rates of dehydration of the mealworms during trials, ultimately resulting in inaccurate measures of consumption. It should be noted, however, that different techniques used in GP studies may yield different GP measures, depending on the digestibility of the material used as a marker.

It could also be argued that the use of beads as markers for GP might have affected our measures of GP and appetite since the indigestible beads occupy a portion of the volume of the stomach and the texture of the bead surface influence passage time in some way. However, the long duration of trials (14 days) is likely to reduce this overall effect, and since our comparisons were relative (same experimental set-up, only temperature was changed), any effect would have little affect on our conclusions. The fact that the lizards also fed freely throughout the trial periods suggests that the effect of the beads was minimal.

## Energy efficiencies

Previously measured ADEs in lizards range between 30% (Ruppert 1980) and 93% (Johnson and Lillywhite 1979). Our measure of 94% for ADE in *C. m. melanotus* thus slightly extends this range. ADEs of insectivores are expected to be in the higher part of the range. Johnson and Lillywhite (1979) recorded an ADE of 93% in *K. riversiana* fed entirely on mealworms (the same diet that we used for our lizards). Many other lizards have similar ADEs when maintained on an exclusively insectivorous diet: *Uta stansburiana* (Waldschmidt et al. 1986); *S. merriami* (Beaupre et al. 1993) and *Hemidactylus turcicus* (Slade et al. 1994).

Although we did not detect a temperature effect on ADE in our study, temperature is known to affect ADE in other species. ADE increases with increasing temperature in *E. elegans*, but asymptotes at 26 °C (Du et al. 2000). However, Du et al. (2000) found no temperature effect on AAE in this species, which suggests that the lack of temperature effects on AAE are due to temperature effects on urate production (i.e. the loss of energy in the form of urates is included in AAE but not in ADE).

## Ecological significance

The digestive physiology of *C. m. melanotus* is well-matched to its feeding strategy and naturally low rates of food intake. Temperature independence of ADE results in the lizards extracting the maximum possible energy from any ingested meal, regardless of whether or not the lizard is able to maintain $T_b$ in the selected range. However, because *C. m. melanotus* has low rates of food consumption under natural conditions (McConnachie and Whiting 2003), the longer time required for digestion at lower temperatures is unlikely to ever limit food intake under these conditions, as may well be the case for frequent feeders or for high consumption feeders. Thus, the digestive physiology of *C. m. melanotus* appears to suit a food-scarce environment by maximising the energy gain from ingested food.

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