Bioenergetic modeling reveals that Chinese green tree vipers select postprandial temperatures in laboratory thermal gradients that maximize net energy intake

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ARTICLE INFO

Article history:
Received 3 February 2009
Received in revised form 8 June 2009
Accepted 15 July 2009
Available online 23 July 2009

Keywords:
Multiple regressions
Feeding frequency
Meal size
Metabolic rate
Specific dynamic action
Rate and efficiency

ABSTRACT

With bioenergetic modeling, we tested the hypothesis that reptiles maximize net energy gain by postprandial thermal selection. Previous studies have shown that Chinese green tree vipers (Trimeresurus s. stejnegeri) have postprandial thermophily (mean preferred temperature \( T_p \) for males = 27.8 °C) in a linear thigmothermal gradient when seclusion sites and water existed. With some published empirical models of digestion associated factors for this snake, we calculated the average rate \( E_{net} \) and efficiency \( K_{net} \) of net energy gain from possible combinations of meal size, activity level, and feeding frequency at each temperature. The simulations consistently revealed that \( E_{net} \) maximizes at the \( T_p \) of these snakes. Although the \( K_{net} \) peaks at a lower temperature than \( E_{net} \), the value of \( K_{net} \) remains high (≥ 0.85 in ratio to maximum) at the peak temperature of \( E_{net} \). This suggested that the demands of both \( E_{net} \) and \( K_{net} \) can be attained by postprandial thermal selection in this snake. In conclusion, the data support our prediction that postprandial thermal selection may maximize net energy gain.

A1. Introduction

Thermoregulation is an activity that indirectly influences fitness by directly affecting physiological, reproductive, and ecological performance (Huey, 1982). The relationship between thermoregulatory behavior and thermal physiology has been a focus of evolutionary physiologists for several decades (Huey, 1982; Dorcas et al., 1997; Angilletta et al., 2002b; Martin and Huey, 2008). A classical hypothesis frequently being tested in physiological ecology holds that the preferred temperatures \( (T_p) \) of ectotherms should be suited of adaptations with and match the optimal temperatures \( (T_{opt}) \) for Darwinian fitness (reviewed in Martin and Huey, 2008). Thermal dependence of Darwinian fitness (on population growth), however, has only been measured in few invertebrates but never in lizards or snakes (Martin and Huey, 2008).

Thermoregulation may necessitate conflict to meet physiological or behavioral traits because different traits may have different thermal optima (Beitinger and Fitzpatrick, 1979; Angilletta et al., 2002b). Animals may select a \( T_b \) that is suboptimal for other traits to optimize the most important needs (Beitinger and Fitzpatrick, 1979; Huey and Stevenson, 1979). Energy processing capacity of reptiles are limited and as such selection should mould their behavior to regulate \( T_b \) for digestive processing maximization including the timing of eating as well as thermal selection during digestion (Congdon, 1989). That is, animals should manipulate its \( T_b \) to maximize energy intake, which is important for its survival, growth, and reproduction (Merker and Nagy, 1984; Nagy, 1989; Stevenson et al., 1985) as well as for Darwinian fitness.

To know whether reptiles maximize net energy gain by thermal selection, we began with experiments in laboratory thermal gradients. The range of \( T_p \) selected by an animal in a laboratory thermal gradient when restrictions on temperature selection are absent is usually assumed to be an estimate of its physiological ‘target range’ (Huey, 1982; Stevenson et al., 1985; Hertz et al., 1993). Hence, it may be more feasible for an animal to maximize the target physiological performance in a laboratory thermal gradient than in the field with many limitations on thermoregulation. Tsai and Tu (2005) measured the temperature selection of adult male Chinese green tree vipers (Trimeresurus s. stejnegeri) in a linear thigmothermal gradient when seclusion sites and water were provided. The snakes did not show a significant circadian rhythm of \( T_b \) in the thermogradient and the preprandial and postprandial \( T_p \) was 22.5 ± 1 °C (means ± SE; \( T_{opt} = 20.3–24.3 \) °C, which are bounds of the central 50% of selected body temperatures) and 27.8 ± 0.6 °C (\( T_{opt} = 26.5–28.8 \) °C), respectively. Chin (2008) revealed the temperature of performing maximum strike velocity of \( T. s. \) stejnegeri was 32 °C. It is clear that postprandial thermal selection of this snake does not aim at strike performance. In another study (Tsai et al., 2008), we have determined effects of temperature and food ration on several digestion associated factors, and developed empirical models for estimating the factors. The results from above studies offer us a good chance to test whether reptiles maximize net energy gain by thermal selection.
Some researchers have published energy budgets or growth rates for fish and investigated the effects of varying body size, temperature, and food ration (Brett, 1971; Elliott, 1982; Cui and Wootton, 1988; Russell et al., 1996), but no corresponding investigations were carried out in reptilian studies on energetics (Kitchell and Windell, 1972; Huey and Slatkin, 1976; Stevenson et al., 1985; Lillywhite, 1987; Grant and Porter, 1992; Reading and Davies, 1996;McCue and Lillywhite, 2002; Dorcas et al., 2004). Pitvipers provide suitable species for examining relationships between temperature and energy expenditure in ectotherms (Beaupre, 2002; Dorcas et al., 2004) because they are primarily ambush predators, spending extended periods of time awaiting potential prey (Reinert et al., 1984; Shine and Sun, 2002; Martins et al., 2002). Huey (1982, pp. 41–42) introduced a simple net energy gain model describing how the selected temperature of reptiles could vary with the amount of ingested food to attain the largest net energy gain. In this model the difference between the benefit from food and the cost from metabolism was considered as net energy gain although it oversimplified digestive/metabolic considerations. By developing Huey’s model, we simulated the net energy gain of T. s. stejnegeri with multiple regression equations from Tsai et al. (2008), and tested whether reptiles maximize net energy gain by thermal selection.

2. Materials and methods

2.1. Factors in the net energy gain model

Data on time and temperature dependence of food consumption, food processing capacity, metabolism, and activity must be acquired to estimate energy budgets (Grant and Porter, 1992). We have determined effects of temperature (15 to 35 °C by 5 °C intervals) and food ration (10, 20 or 30%) on several digestion associated factors (Tsai et al., 2008), including standard metabolic rate (SMR), specific dynamic action (SDA), SDA duration (duration of SDA response), and apparent assimilation energy (= total consumed energy minus energy lost in feces and uric acid) in the mature male Chinese green tree viper. Empirical models for estimating the factors were developed with predator variables including snake mass, mouse mass, and temperature (see Table 1). All possible interacting terms were initially included in the full model which was fit to the data using the backward regression procedure and criteria of partial F statistics to reduce the number of predictor variables where possible (Cui and Wootton, 1988; Neter et al., 1999). We checked whether significantly influencing outliers existed in the data by the criteria of h^2 and Cooper’s D^2 statistic (Neter et al., 1999). The success of the model was judged by minimizing the difference between Mallows’s Cp statistic and the number of parameters in the model (Beaupre et al., 1993) as well as the values of r^2 and PRESSp statistics (Neter et al., 1999). In addition, to further verify the regression models, we compared real data on SDA-associated factors of T. s. stejnegeri at 24 °C from another study (N = 8; Chu et al., 2009) with the corresponding simulated data from our regression models. The real data were not significantly different from the simulated ones (paired r-test; means ± SE of log SMR = 0.30 ± 0.04 vs. 0.25 ± 0.02 mL O2/h, P = 0.31; log SDA = 2.52 ± 0.05 vs. 2.50 ± 0.03 mL O2, P = 0.44; log SDA duration = 0.80 ± 0.02 vs. 0.85 ± 0.01 d, P = 0.09). The simulations effectively reflected real data and the regression models were used to simulate the energy budget model in this study. Further considerations of these factors in estimating E\text{net} or K\text{net} are described below.

2.1.1. Food consumption and food processing capacity

Total food consumption in a unit of time is equal to meal size in each feeding bout multiplied by feeding frequency during this time. On a twig, T. s. stejnegeri generally cannot successfully bite a mouse with mass greater than 33% of the snake's mass (Tsai, 2007). Due to this reason, we set meal size below 30% of the snake’s mass in each feeding bout. We assumed that only one mouse could be eaten in each feeding and that snakes did not feed on a second mouse until the first meal has been completely processed (Beaupre, 2002). Because SDA is believed to be a sum of energy required for muscle activity (peristalsis), secretary processes, protein catabolism, active transport (nutrient uptake), protein synthesis, and nitrogenous waste excretion (McCue and Lillywhite, 2002; Secor, 2003), we set SDA duration as digestion time (Tsai et al., 2008) in the energy model. Food processing capacity was assayed by determining assimilation efficiency, that is, proportion of energy extracted from food.

2.1.2. Energetic costs during feeding and digestion period

Pitvipers (including arboreal species) may capture their prey from ambush sites, with individual snake sometimes remaining in the same site for days or weeks (Reinert et al., 1984; Shine and Sun, 2002; Martins et al., 2002). It has also been found that Chinese green tree vipers spent several days (sometimes up to 2 weeks) around the same ambush site waiting for prey (Lin et al., 2007). Therefore, energetic costs from complicated behaviors were not considered in our energy model. We considered the energetic costs in two phases: during feeding and digestion vs. during non-digestion. Energy costs during feeding and digestion period include those from prey handling, ingestion, and digestion process as well as baseline metabolism. Baseline metabolism was calculated from SMR. Energy costs of prey handling and ingestion in fish, lizards, and snakes, when compared to the net assimilated energy of the prey, are small or seem negligible (Andrade et al., 1997; Cruz-Neto et al., 2001; Canjani et al., 2003). For example, the energy cost of ingestion was only 0.003–0.02% the total energy content of prey of juvenile South American rattlesnake (Crotalus durissus: Cruz-Neto et al., 1999). In contrast, the energy cost of digestion is prominent. Field and laboratory studies have shown that SDA is an important component of the energy budget for snakes (Secor and Phillips, 1997). Because T. s. stejnegeri has little activity after feeding (during digestion) in the laboratory (Tsai and Tu, 2005), we determined SDA and baseline metabolism as the main energy costs during feeding and digestion in the basal settings (see Section 2.3.2).

2.1.3. Energetic costs during non-digestion period

Snakes are well known for their sedentary behavior and long periods of seclusion. Many routine activities are perceived as low and deliberate (Lillywhite, 1987), although the cumulative energy expended might be considerable (Huey, 1982). Many reptiles under natural conditions are

<table>
<thead>
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<th>Table 1</th>
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<tr>
<th>Regression formula</th>
<th>CP</th>
<th>PRESSp</th>
<th>r^2</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log SMR (mL O2 h⁻¹) = −2.056 + 0.0407 + 0.767 log SM</td>
<td>2.44</td>
<td>0.75</td>
<td>0.87</td>
<td>208.00</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log SDA (mL O2) = 1.704 + 1.049 log MM</td>
<td>2.77</td>
<td>0.77</td>
<td>0.76</td>
<td>188.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log SDA (day) = 2.771 − 0.136T + 0.0202T^2 + 0.285 log MM</td>
<td>2.84</td>
<td>0.64</td>
<td>0.88</td>
<td>151.14</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log E\text{fes} (J) = 3.000 + 0.033T − 0.00067T^2 + 1.385 log MM</td>
<td>4.64</td>
<td>0.06</td>
<td>0.99</td>
<td>1881.71</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log E\text{max} (J) = 3.576 + 1.234 log MM</td>
<td>4.06</td>
<td>0.01</td>
<td>0.91</td>
<td>125.52</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Note. The regression models included those for standard metabolic rate (SMR), specific dynamic action (SDA), SDA duration (T\text{fes}), and apparent assimilation energy (E\text{fes}) as well as mouse energy (E\text{max}), with temperature (T, °C), mouse mass (MM, g) or snake mass (SM, g) as independent variables. The energy equivalent is 19.8 J/mL O2 (Gessaman and Nagy, 1988).
inactive for long portions of the daily cycle. Their rates of energy expenditure during these times may be a little above the metabolic rates measured at rest in the laboratory (Bennett, 1982). McCue and Lillywhite (2002) noted that metabolic rates of cottonmouth snakes (Agkistrodon piscivorus conanti) doubled during periods of slow crawling inside metabolic chambers. The activity metabolism was assumed to be two times standard (baseline) metabolism in garter snakes (Thamnophis elegans; Stevenson et al., 1985). If no digestion was occurring, total energy cost in generic rattlesnake simulation (Beaupre, 2002) was assumed to be 2.0–3.6 (among seasons) times baseline metabolism. Male T. s. stejnegeri, like another arboreal pit-viper (Gloydius shedaoensis; Shine et al., 2003; moving distance was <2 m/day on average during active seasons), showed much less activity (4.9 m/day on average during active seasons by thread-bobbin tracking method; Shiau, 2000) than other terrestrial crotalids (49.0, 48.7, 32.7, 21.3, and 117.8 m/day on average during active seasons for Crotalus atrox, C. molossus, C. tigris, C. horridus, and C. cerastes, respectively; Reinert and Zappalorti, 1988; Secor, 1994; Beck, 1995). Consequently, we set 1–3 times standard metabolism for energy costs during non-digestion period. However, grasping tree branches needs energy and it will likely be more expensive on energetics for arboreal locomotion than for terrestrial one, although energetic studies on this issue have not been found. A larger multiple of standard metabolism was also simulated in sensitivity analysis (see Section 2.3.2).

2.2. Simulations of rate and efficiency of net energy gain

2.2.1. Developing the energy budget model

Organisms may face the conflicting demands of the need to feed and to avoid reducing individual’s fitness (e.g., predation) while feeding (Schoener 1971; Sih 1980). A snake having efficient energy intake would reduce feeding frequencies and probabilities of exposing itself to predators. We therefore evaluated the energy budget from both the rate of net energy gain ($E_{net}$) and the efficiency of net energy gain ($K_{net}$). Using acquired regression equations, we developed an energy budget model to simulate $E_{net}$ and $K_{net}$ of T. s. stejnegeri and under certain meal sizes, feeding frequencies, and activity levels. The energy budget in an entire month was considered at two periods (digestion and non-digestion), which was analyzed as follows.

The monthly maximal net energy gain is

$$E_{net} = \text{energy gain from food} − \text{energy cost during digestion} − \text{energy cost during non-digestion}. \tag{1}$$

In which,

$$\text{Energy gain from food} = E_{\text{mouse}} \times f \tag{2}$$

$$\text{Energy cost during digestion} = \text{energy cost from baseline metabolism and SDA} \tag{3} = (E_{\text{met}} \times 24 \times T_{\text{SDA}} + E_{\text{SDA}}) \times f$$

$$\text{Energy cost during non-digestion} = \text{energy cost from baseline metabolism and activity} \tag{4} = E_{\text{met}} \times 24 \times (30 − (T_{\text{SDA}} + f)).$$

By substituting formulae (2), (3), and (4) for formula (1), we get

$$E_{\text{net}} = (E_{\text{mouse}} − ((E_{\text{met}} \times 24 \times T_{\text{SDA}} + E_{\text{SDA}})) \times f − (E_{\text{met}} \times 24 \times 30 − (T_{\text{SDA}} + f)). \tag{5}$$

Efficiency of net energy gain is

$$K_{\text{net}} = \frac{\text{monthly maximal net energy gain}}{\text{energy of ingested mouse}} \tag{6}$$

In addition, two types of feeding frequency could be calculated to estimate the potential scope of feeding dynamics. One is maintenance feeding frequency ($f_{\text{main}}$), which is the feeding frequency when $E_{\text{net}}$ is equal to zero. The formula to calculate $f_{\text{main}}$ is

$$f_{\text{main}} = \frac{(E_{\text{met}} \times 24 \times 30)}{(E_{\text{mouse}} − E_{\text{SDA}} − (E_{\text{met}} \times 24 \times T_{\text{SDA}}) + (E_{\text{met}} \times 24 \times I_{\text{act}} \times T_{\text{SDA}})).} \tag{7}$$

The maximal permitted feeding frequency ($f_{\text{max}}$) is

$$f_{\text{max}} = \frac{30}{T_{\text{SDA}}} \tag{8}$$

where $E_{\text{mouse}}$ is the total energy of one mouse (J; see Table 1), $E_{\text{mouse}}$ is assimilated energy extracted from digesting one mouse, $E_{\text{net}}$ is energy costs from baseline metabolism during digestion (J h\(^{-1}\)), $E_{\text{net}}$ is energy costs from baseline metabolism at 22.5 °C (during non-digestion; J h\(^{-1}\)), $f$ is feeding frequency (mon\(^{-1}\)), $T_{\text{SDA}}$ is SDA duration (day), $E_{\text{SDA}}$ is energy cost from SDA (J), and $I_{\text{act}}$ is activity level (ex. 1–3). Energy cost during non-digestion was set as the product of activity level and baseline metabolic costs. Examples of the relationships among temperature, $I_{\text{act}}$, and $f_{\text{main}}$ or $f_{\text{max}}$ are illustrated in Fig. 1.

2.2.2. Simulations with energy budget model

Because an analytical solution for above equations, substituted by corresponding regression models, does not exist, we ran numerical simulations (Martin and Huey, 2008) in Microsoft Excel. In simulations, snake mass was set to 50 g and mouse mass was 5, 10, and 15 g (i.e., 10, 20, and 30% food ration). Only one mouse can be eaten in each feeding and the snake does not have another feeding until digestion is completed (Beaupre, 2002). The snake’s $T_{\text{b}}$ during non-digestion period was assumed as 22.5 °C, which was the mean preprandial $T_{\text{b}}$. From this point, the feeding frequency was calculated.
in a thermogradient (Tsai and Tu, 2005). The snake’s $T_b$ during digestion was simulated at 15–35 °C by 0.1 °C intervals. When considering possible variations on food resource/intake in nature, we set a series of upper limits of feeding frequency ($f_{\text{lim}} = 1, 2, 3,...$) to simulate the variable conditions of limiting food intake. Examples of the relationships among temperature, $f_{\text{lim}}$, and $E_{\text{net}}$ or $K_{\text{net}}$ are illustrated in Fig. 2. To signify thermal sensitivity of $E_{\text{net}}$ or $K_{\text{net}}$, we calculated a 95% thermal performance breadth of $E_{\text{net}}$ or $K_{\text{net}}$ (Baz; Huey and Bennett, 1987; Angilletta et al., 2002a).

2.3. Temperature attaining largest $E_{\text{net}}$ or $K_{\text{net}}$

2.3.1. Algorithms

Exact conditions of meal size, feeding frequency, and activity of $T. s. stejnegeri$ in the field are still unknown. Therefore, we calculated the optimal temperature for $E_{\text{net}}$ or $K_{\text{net}}$ by considering all possible combinations of variables (meal size, activity level, and feeding frequency) to verify whether the snakes acquired the largest $E_{\text{net}}$ or $K_{\text{net}}$ by temperature selection. We first calculated $E_{\text{net}}$ at each temperature under certain combinations of meal size, activity level, and feeding frequency. Then, for each temperature, the $E_{\text{net}}$s calculated at all combinations of meal size, activity level, and feeding frequency were summed up (i.e., $\Sigma E_{\text{net}}$) and divided by number of combinations to get average $E_{\text{net}}$. Average $K_{\text{net}}$ was calculated as $\Sigma E_{\text{net}}$ divided by total $E_{\text{mouse}}$. In these simulations, mouse mass was set as 5 to 15 g by 0.1 g intervals, and activity level was set as 1.0 to 3.0 by 0.1 intervals. Mao (1970) found that 2 to 14% of $T. s. stejnegeri$ had food in their stomach at different seasons by inspecting the specimens collected in the field. This snake may have a low feeding frequency in the field. Besides, the potential $f_{\text{max}}$ is 4.8 times per month (calculated at 30% meal size). Therefore we set feeding interval as one week to three months by 1 day intervals, that is, feeding frequency was set as 0.33 (=30/90) to 4.5 (=30/7) times per month in the basal settings (see Section 2.3.2). Calculations of average $E_{\text{net}}$ or average $K_{\text{net}}$ involved a large array of parameters and were conducted with the Perl dynamic program.

2.3.2. Sensitivity analysis

Except the basal settings mentioned above, we also examined the effects of variation in selected input variables on $E_{\text{net}}$ or $K_{\text{net}}$ using a sensitivity analysis (Beaupre, 2002). First, the activity level in the original energy model was set even higher (=1–5) by considering a larger energy cost for arboreal locomotion. Second, the feeding interval was set even longer (from 3 months to 4 months, that is, feeding frequency was set as 0.33 (=30/90) to 4.5 (=30/7) times per month in the basal settings (see Section 2.3.2). Calculations of average $E_{\text{net}}$ or average $K_{\text{net}}$ involved a large array of parameters and were conducted with the Perl dynamic program.

The simulated $E_{\text{net}}$ or $K_{\text{net}}$ from above modifications was compared to those of the original model (Eq. (5)) and settings.

3. Results

3.1. General trends of simulated variables

Several trends of simulated variables ($f_{\text{max}}, f_{\text{lim}}, E_{\text{net}},$ and $K_{\text{net}}$) on meal sizes, temperatures, activity levels, or feeding frequency can be summarized. Although many trends were potentially artifacts of simplifying assumptions of the model, some were consistent with previous studies in fish (Cui and Wootton, 1988; Russell et al., 1996). For example, (1) the predicted maintenance and maximum food intake increased with temperature (Figs. 1 and 2) when feeding frequencies were increased, and (2) both $E_{\text{net}}$ and $K_{\text{net}}$ were peaked at higher temperatures (Fig. 2).
3.2. Temperatures attaining largest $E_{\text{net}}$ or $K_{\text{net}}$

The average $E_{\text{net}}$ or $K_{\text{net}}$ calculated from all combinations of possible meal sizes, activity levels, and feeding frequencies at each temperature was presented as relative (ratio of maximum) values in Fig. 3. By simulating with the basal model (Eq. (5)) and basal settings, the $E_{\text{net}}$ peaked at 27.6 °C ($B_{95} = 24.4–30.6$ °C; Fig. 3A) and was around the mean postprandial $T_p$ (27.8 °C; Tsai and Tu, 2005), while the $K_{\text{net}}$ peaked at 24.6 °C ($B_{95} = 19.3–28.9$ °C; Fig. 3A). At the $T_o$ of $E_{\text{net}}$, the relative value of $K_{\text{net}}$ was 0.97. At the $T_o$ of $K_{\text{net}}$, the relative value of $E_{\text{net}}$ was 0.95. When the activity level was set even higher (as high as 5; other variables unmodified), $K_{\text{net}}$ peaked at far lower temperatures; the $E_{\text{net}}$ peaked at 26.7 °C while the $K_{\text{net}}$ peaked at 15.7 °C. When the feeding frequency was set lower (as low as 30/120; other variables unmodified), both indices were not changed significantly; the $E_{\text{net}}$ peaks at 27.2 °C while the $K_{\text{net}}$ peaked at 24.9 °C. When both activity level and feeding frequency were modified as above, $K_{\text{net}}$ again peaked at far lower temperatures; the $E_{\text{net}}$ peaked at 26.1 °C while the $K_{\text{net}}$ peaked at 15.0 °C (Fig. 3B). At the $T_o$ of $E_{\text{net}}$, the relative value of $K_{\text{net}}$ was 0.89. At the $T_o$ of $K_{\text{net}}$, the relative value of $E_{\text{net}}$ was 0.62. The differences between mean postprandial $T_p$ and $T_o$ of $E_{\text{net}}$ in above four conditions ranged between 0.2 and 1.7 °C.

By simulating with the modified model (Eq. (9)) and basal settings, the simulated curve for $E_{\text{net}}$ was closer to that for $K_{\text{net}}$ (Fig. 3C). The $E_{\text{net}}$ peaked at 28.2 °C ($B_{95} = 25.6–30.9$ °C), while the $K_{\text{net}}$ peaked at 26.9 °C ($B_{95} = 23.8–29.9$ °C). Similar results were found when the settings of

![Fig. 3](image-url)
activity level or the feeding frequency were modified as above. If the activity level was set higher, the $E_{\text{net}}$ peaked at 27.9 °C while the $K_{\text{net}}$ peaked at 27.0 °C. If the feeding frequency was set lower, the $E_{\text{net}}$ peaked at 28.0 °C while the $K_{\text{net}}$ peaked at 27.0 °C. If both activity level and feeding frequency are modified, the simulated curves for $E_{\text{net}}$ and $K_{\text{net}}$ nearly overlapped (Fig. 3D) and both indices were around the mean postprandial $T_p$. The $E_{\text{net}}$ peaked at 27.6 °C while the $K_{\text{net}}$ peaked at 27.2 °C. The differences between mean postprandial $T_p$ and $T_b$ of $E_{\text{net}}$ in above four conditions were all smaller than 0.4 °C.

4. Discussion

The simulated average $E_{\text{net}}$ (even under modifications of the energy model or parameter settings) consistently reveals that Chinese green tree vipers select postprandial temperatures in laboratory thermal gradients that maximize net energy intake. The average $E_{\text{net}}$ peaks around postprandial $T_p$ ($\text{mean} = 27.8^\circ \text{C}$) of $T. s. \text{stejnegeri}$, and the difference between mean $T_p$ and $T_b$ of $E_{\text{net}}$ may be smaller than 0.2 °C. Recently, Martin and Huey (2008) demonstrated in theory that $T_p$ will be below $T_b$ for fitness when the fitness-temperature curves present dominant asymmetry or high thermal sensitivity (i.e., for thermal specialist). It has been found that the mean critical thermal minimum and maximum of $T. s. \text{stejnegeri}$ is 5.6 and 38.9 °C, respectively (Huang et al., 2007). We calculated the asymmetry ($\pm 0.32$) of $E_{\text{net}}$ curve in Fig. 3A, by the formula presented in Martin and Huey (2008). According to the simulations in Martin and Huey (2008), $T_p$ will be equal to $T_b$ for fitness when asymmetry is below 0.4, which was also evident in our simulations. In short, the data support our prediction that net energy gain is maximized by thermoregulation and it should be regarded as an appropriate indicator to Darwinian fitness.

The simulated $K_{\text{net}}$ in the basal energy model (Eq. (5)) peaks at lower temperatures than $E_{\text{net}}$ while the two indices peak at similar temperatures when simulated in the modified model (Eq. (9)). The $K_{\text{net}}$ does not decrease very much around the postprandial $T_p$ of the snake; at the $T_o$ of $E_{\text{net}}$, the relative value of $K_{\text{net}}$ generally attains 0.85. In contrast, at the $T_o$ of $K_{\text{net}}$, the relative value of $E_{\text{net}}$ may be as low as 0.62 (Fig. 3B). Selecting low temperatures after feeding may increase $K_{\text{net}}$; however, it will also lower the rate of energy gain and growth/ reproduction. Tree vipers’ arboreal behavior, linked with their green coloration and sedentariness within branches and foliage, enhances their protection as they may go unnoticed by predators even as they rest in the upper canopy of vegetation structures during the day (Lin et al., 2007). Based on observations of two nesting pairs of crested serpent eagles (Spilornis cheela) during their entire brooding period, of the 65 recorded instances where snakes were taken as food for their chicks, only two episodes involved green tree vipers (cited in Lin et al., 2007). Due to the potential lower predation pressure the snakes therefore mainly maximize $E_{\text{net}}$ but not $K_{\text{net}}$ by postprandial thermophily. In fact, complete requirements to meet a trade-off between rate and efficiency of energy gain (Elliott, 1982; Angilletta et al., 2002b) in this study were not evident. It would be a more realistic result that the snakes can roughly satisfy the demands on rate and efficient of energy gain by selecting higher temperatures after feeding.

No mathematical model can duplicate a natural system, yet relatively simple models often capture essential features of the biological systems they describe, leading to insights unattainable through empirical means alone (Hom, 1988). Numerous studies (e.g., Hom, 1988; Grant and Porter, 1992) have used diverse optimization techniques to generate hypotheses about life historical time and energy allocation, although some factors might not be considered (Huey, 1982, 1991). Running a quantitative test of life history theory may predict the mean $T_p$ that would optimally compromise between conflicting thermal optima (Beuchat and Ellner, 1987). However, a similar test cannot be carried out because adequate life history information, such as survivorship or reproductive success, is not available for $T. s. \text{stejnegeri}$. In addition, the equations in this study did not run for every hour of the day because the digestion associated factors (e.g., SDA, SDA duration, and assimilation energy) in Tsai et al. (2008) were assayed from the snakes digesting at constant temperatures. We do not know what the values of these factors would be for the snakes digesting at fluctuating temperatures. For the nonlinear progressing on digestive performance during the entire digestion period, it would make errors to simulate digestion associated factors at hourly-changing temperatures with the regressions obtained at constant temperatures. More studies on digestion at fluctuating temperatures should be necessary before we can set up an hourly energy model for $T. s. \text{stejnegeri}$.

The thermal regimes selected by an ectotherm are in fact dynamic and vary with factors such as body condition, health, reproductive status, water balance, sloughing stage, acclimation, and diurnal and seasonal rhythms (Huey, 1982). The behavior of an animal in a simplified environment such as a laboratory thermal gradient may not accurately represent its activities in the wild (Wall and Shine, 2008). By now it is difficult to extrapolate our laboratory findings to the field because little is known about the field ecology of these snakes. Many snakes have a $T_p$ within the range of 28 to 34 °C, only some fossorial, secretive, or nocturnal snakes show $T_p$ below 25 °C (cited in Tsai and Tu, 2005). The annual mean temperature (screen-level air temperature) in lowland of northern Taiwan is about 22.5 °C (see Fig. 1 in Tsai and Tu, 2001; Chen, 2008), which just fit the preprandial $T_p$ of $T. s. \text{stejnegeri}$. Lin et al. (2007) found that when the ambient temperature is higher than 25 °C, which is just higher than the preprandial $T_{\text{net}}$ of this snake, $T. s. \text{stejnegeri}$ (preprandial) in outdoor enclosures prefer to retreat into denser vegetation for significantly lower shaded temperatures. The snakes may also select similar preprandial $T_p$ in the field as in lab. Nocturnal animals would not be expected to show a diel cycle in mean $T_p$ (cited in Tsai and Tu, 2005). The circadian variation of $T_p$ was not considered in the model because the snakes showed no circadian rhythm of $T_p$ in laboratory experiments of thermal selection. The annual mean temperature of day and night time is 24 and 21 °C in Taiwan (Tsai and Tu, 2001; Chen, 2008). It is possible that in the field the $T_p$ is different between day and night. The seasonal (spring–winter) mean temperature in Taipei is 21.2, 28.2, 24.2, and 16.3 °C (calculated from Fig. 1 in Tsai and Tu, 2001). The snakes may easily find proper thermal patches to digest in summer, and need to spend more time to find proper microhabitats to digest in other seasons. Until now we cannot make sure whether the nocturnal $T. s. \text{stejnegeri}$ seek warmer temps after feeding once the sun rises in the field.

There are good opportunities for building a neat system by integrating simulations with empirical data (Beaupre, 2002; Butler et al., 2004) of $T. s. \text{stejnegeri}$ in the wild. To attain this goal, information of temperature selection, activity, and energy budget of $T. s. \text{stejnegeri}$ in the field is needed. Projects on thermal selection and energetics of Chinese green tree vipers in wild are proceeding. With proper field data including food resources, we could calculate the maintenance food ration or feeding frequency of this snake and predict the geographical distribution pattern of this snake in Taiwan. It also may explain why this snake is much more abundant in certain local area of Taiwan. In addition, Chinese green tree viper is widely distributed in southern China, Taiwan, India, Laos, Thailand, and Vietnam (Zhang and Adler, 1993), making it an appropriate species to study site effects (Grant and Porter, 1992). With essential background information, evolutionary adaptations on energy budgets and other factors for snakes in different geographical areas can be predicted and investigated.

Acknowledgements

We thank H.B. Lillywhite and anonymous reviewers for commenting on an early version of the manuscript. We are especially grateful to YJ. Tian for instructions in the Perl dynamic program. Our gratitude also
goes to the Academic Paper Editing Clinic, NTNU. This research was financially supported by the National Science Council, ROC (NSC 92-2311-B-003-002).

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