

Ontogenetic shifts in thermal tolerance, selected body temperature and thermal dependence of food assimilation and locomotor performance in a lacertid lizard, *Eremias brenchleyi*

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Abstract

We used *Eremias brenchleyi* as a model animal to examine differences in thermal tolerance, selected body temperature, and the thermal dependence of food assimilation and locomotor performance between juvenile and adult lizards. Adults selected higher body temperatures (33.5 vs. 31.7 °C) and were able to tolerate a wider range of body temperatures (3.4–43.6 vs. 5.1–40.8 °C) than juveniles. Within the body temperature range of 26–38 °C, adults overall ate more than juveniles, and food passage rate was faster in adults than juveniles. Apparent digestive coefficient (ADC) and assimilation efficiency (AE) varied among temperature treatments but no clear temperature associated patterns could be discerned for these two variables. At each test temperature ADC and AE were both higher in adults than in juveniles. Sprint speed increased with increase in body temperature at lower body temperatures, but decreased at higher body temperatures. At each test temperature adults ran faster than did juveniles, and the range of body temperatures where lizards maintained 90% of maximum speed differed between adults (27–34 °C) and juveniles (29–37 °C). Optimal temperatures and thermal sensitivities differed between food assimilation and sprint speed. Our results not only show strong patterns of ontogenetic variation in thermal tolerance, selected body temperature and thermal dependence of food assimilation and locomotor performance in *E. brenchleyi*, but also add support for the multiple optima hypothesis for the thermal dependence of behavioral and physiological variables in reptiles.

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1. Introduction

Reptiles have the potential to maintain relatively high and constant body temperatures through behavioral thermoregulation when temporally and spatially variable heat sources are available (Cowles and Bogert, 1944). However, in uniform thermal environments such as underground, underwater, and deeply shaded forests, behavioral thermoregulation is constrained and, for species whose physiological thermoregulation

is very limited or even negligible, variation in body temperature typically tracks variation in ambient temperature (Bartholomew, 1977; Wang and Xu, 1987; Ji et al., 2002; Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003; Lin et al., 2005). Uniform thermal environments can be established in the laboratory, where a reptile's body temperatures can be controlled so that the upper and lower limits of thermal tolerance and functional capabilities can be examined at any given body temperature. Data generated from laboratory studies show that the thermal optima and thermal sensitivities of individual functional capacities may vary among and within species (e.g., Van Berkum, 1986; Waldschmidt et al., 1986; Van Damme et al., 1991; Witz and Lawrence, 1993; Ji et al., 1995, 1996a; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004). Moreover, inter-specific comparisons reveal that reptiles living in different

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habitats and geographic or climatic regions select different body temperatures and differ considerably in thermal tolerance (Jaksic and Schwenk, 1983; Paulissen, 1988a; Grant and Dunham, 1990; Lemos-Espinal and Ballinger, 1995; Andrews, 1998; Melville and Schulte, 2001; Zhang and Ji, 2004).

Over the past few decades, studies on thermally sensitive behavioral and physiological variables in reptiles have focused more on food assimilation and locomotor performance than on other variables. These two ecologically relevant variables can be easily measured and are associated closely with an individual's fitness. For example, net energy gains achieved from feeding can be allocated to somatic tissue growth and production of offspring (Nagy, 1983), whereas locomotor performance is of importance for avoiding predators and enhancing foraging success (Pough, 1989; Bauwens et al., 1995; Miles et al., 1995; Shine, 2003). However, few studies have examined ontogenetic differences in either food assimilation (but see Ji et al., 1995; Xu et al., 1999) or locomotor performance (but see Irschick, 2000; Irschick et al., 2000). As juvenile and adult animals differ not only in morphology but also in habitat use, behavior, and functional capacities, examination of differences in behavioral and physiological variables between individuals in different age classes in a population is critical to understanding how ecological communities are structured (Werner and Gillam, 1984; Irschick et al., 2000).

Here, we present data on thermal tolerance [critical thermal minimum (CT_{\min}) and critical thermal maximum (CT_{\max})], selected body temperature (T_{sel}), and the thermal dependence of food assimilation and locomotor performance in *Eremias brenchleyi*. This small (up to 69 mm snout-vent length; Xu and Ji, 2003), oviparous, heliothermic lacertid lizard is endemic to China and lives in several eastern and northern provinces of the country (Chen, 1991). It is typically found in open sunny spaces in hilly countryside covered with sparse vegetation, rock fragments, and gravels (Chen, 1991). Adults do not exhibit sexual dimorphism in body size, and large females can lay up to four clutches per breeding season, which normally lasts from May to July (Xu and Ji, 2003). The lizard exhibits a non-random selection of thermal microhabitats (Chen, 1991), and is ideally suited to our investigation. Our aims were (1) to test for ontogenetic shifts in thermal tolerance, selected body temperature, and the thermal dependence of food assimilation and locomotor performance, and (2) to evaluate the significance of ontogeny in the examined variables and multiple thermal optima for performance.

2. Materials and methods

2.1. Collection and animal care

Adult males (55.5–64.7 mm SVL), non-reproductive females (56.2–65.3 mm SVL), and juveniles (40.3–47.5 mm SVL) of *Eremias brenchleyi* were collected in early April of 2003 and 2004 from a population in Suzhou (Anhui, eastern China), approximately 15 d following winter dormancy. The lizards were transported to our laboratory at Chuzhou

University, where they were individually sexed, weighed, and measured. Lizards smaller than 50 mm SVL were classified as juveniles (Xu and Ji, 2003). Prior to the experiment and during intervals of trials, 8–10 lizards were maintained in a 100×80×50 cm glass terrarium, with moist soil, grasses, and pieces of clay tiles. We fed lizards mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals. Supplementary heating was provided by a 250-W light bulb suspended 15 cm above the terrarium floor and the light cycle was programmed to simulate natural condition, allowing behavioral thermoregulation.

2.2. Selected body temperature and thermal tolerance

We measured T_{sel} , CT_{\min} , and CT_{\max} in mid-April of 2003 and 2004, and the experimental sequence was T_{sel} , CT_{\min} , and CT_{\max} at intervals of a week to reduce possible interferences between experiments. Prior to each experiment, lizards were maintained at 28 °C for 48 h to habituate the starting temperature.

Selected body temperatures of 33 lizards (17 juveniles and 16 adults) were determined in a 100×80×50 cm glass terrarium with 5 cm depth moist soil and pieces of clay tiles. Two light bulbs (total 500 W) suspended above one end of the terrarium created a thermal gradient ranging from ambient room temperature to 60 °C for 12 h daily. Lizards were moved from the cool side into the terrarium at 0730 when the lights were switched on. Because there might be diel variation in T_{sel} (Hutchison, 1976), we began all measurements at 1500 and ended within 2 h, thereby making our data comparable to those collected in the same manner for other species of lizards. Active lizards in the thermal gradient were picked up and body temperatures (cloacal, T_b) were measured using the external thermal probe (1 mm diameter) of a WMZ-03 electronic thermometer (Shanghai Medical Instruments, China), which had been calibrated with a standard thermometer. Great care was taken to minimize any heat transfer between hands and lizards when handling them for measurements. To address the repeatability of our measurements, we measured each lizard twice, once on each of two consecutive days. A paired-sample *t*-test showed that the two measures were similar in both adults ($t=0.52$, $df=15$, $P=0.611$) and juveniles ($t=1.64$, $df=16$, $P=0.121$); we therefore used the mean of the two measures as an individual's selected body temperature.

CT_{\min} and CT_{\max} (12 juveniles and 15 adults) were determined using a PYX-250S-A incubator (Guangdong Keli Instruments, China). Experiments were conducted during 1000–1500. We cooled (for CT_{\min} determination) or heated (for CT_{\max} determination) lizards from 28 °C at a rate of 0.25 °C min^{-1} and at a slower rate of 0.1 °C min^{-1} when temperatures inside the incubator were lower than 8 °C or higher than 38 °C. During the experiments, we observed the behavior of lizards through a cat-eye in the incubator door. Body temperatures associated with a transient loss of the righting response (individual lizards were not able to reverse when they were turned over) at the lower and the upper limits of thermal tolerance were considered to be the endpoints for CT_{\min} and

CT_{max} , respectively (Ji et al., 1995). One juvenile and five adults died in two weeks following the CT_{max} measurement, probably because the endpoints were exceeded during the experiment.

2.3. Food passage time, food intake, and food assimilation

A total of 133 lizards (10 adults and 9 juveniles at each test temperature) were moved into seven temperature-controlled rooms, where mean body temperatures were experimentally controlled constant at 26, 28, 30, 32, 34, 36, and 38 (± 0.5) °C, respectively. The fluorescent tubes in the constant temperature rooms were on a 12 L:12 D cycle, and the photophase started at 0700 h. Lizards were housed individually in 25 × 15 × 25 cm glass terraria. We fasted lizards at the test temperature for 3 d prior to feeding to ensure post-absorptive conditions, and then fed each lizard two mealworms marked individually with a 3-mm red plastic thread (diameter 0.2 mm) inserted into the larvae's body. We allowed lizards to eat the marked mealworms voluntarily to avoid force-feeding; we subsequently fed them unmarked mealworms and provided water *ad libitum*. We collected feces and urates at least six times daily, and more frequently during the first 3 days, thereby enabling us to collect our food tags within a few minutes after they were expelled. Food passage time was defined as the time from swallowing to the first appearance of plastic threads (Ji et al., 1995). Trials lasted for 18–28 d so that sufficient feces and urates could be collected for calorimetry. The initial body mass was recorded at the end of 3-d fast prior to feeding, and the final body mass was recorded following another 3-d fast at the end of each trial.

Feces, urates, and mealworms corresponding to each lizard were dried to constant mass at 65 °C and weighed. Dried samples were burnt in a WGR-1 adiabatic calorimeter (Changsha Instruments, China), and data were automatically downloaded to a computer. The assimilation efficiency was calculated as $AE = 100 \times (I - F - U) / I$ (Ji et al., 1993), where I = total energy consumed, F = energy in feces and U = energy in urates. The apparent digestive coefficient was calculated as $ADC = 100 \times (I - F) / I$ (Waldschmidt et al., 1986).

2.4. Locomotor performance

A total of 19 lizards (10 adults and 9 juveniles) were measured for locomotor performance at nine body temperatures ranging from 22 to 38 (± 0.5) °C. Individual lizards were used at all the nine test temperatures. The trial sequence was randomized across temperatures (30, 22, 28, 34, 26, 36, 24, 38 and 32 °C). We achieved body temperatures at the test level by placing lizards into an incubator at the corresponding temperatures for approximately 3 h prior to each trial. Lizards were chased with a paint brush down the length of a 150 × 10 × 15 cm wood racetrack with one side panel transparent, which allows lateral filming with a Panasonic NV-MX3 digital video camera. Each lizard was sprinted twice at each test temperature with a 30-min rest between trials; experimental lizards were given a 24-h rest between temperature trials. The

tapes were examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 25 cm interval.

2.5. Statistical analyses

There were no significant between-sex differences in all examined variables, so we pooled the data for both sexes; there were no between-year differences in all examined variables, so we pooled data for both years. All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (F -max test), and arc-sine (for ADC and AE) and \log_e (for other traits when necessary) transformations were performed to satisfy the assumptions for using parametric analyses. We used one-way ANOVA (for the differences in T_{sel} , CT_{min} , and CT_{max} between adults and juveniles), two-way ANOVA (for food passage time, daily food intake, ADC and AE), two-way ANCOVA (for final body mass with initial body mass as the covariate), and repeated measures ANOVA [for locomotor performance with age (juvenile and adult) as the between-subject factor and body temperature as the within-subject factor] to analyze the corresponding data. Descriptive statistics were presented as mean \pm 1 standard error, and the significance level was set at $\alpha = 0.05$.

3. Results

3.1. T_{sel} , CT_{min} , and CT_{max}

T_{sel} was higher in adults than in juveniles (33.5 ± 0.3 vs. 31.7 ± 0.2 °C; $F_{1,31} = 8.87$, $P < 0.006$); CT_{min} was lower (3.4 ± 0.2 vs. 5.1 ± 0.3 °C; $F_{1,25} = 29.63$, $P < 0.0001$) and CT_{max} (43.6 ± 0.2 vs. 40.8 ± 0.2 °C; $F_{1,19} = 93.33$, $P < 0.0001$) was higher in adults than in juveniles (Fig. 1). These results indicate that adults select higher body temperatures and can tolerate a wider range of body temperatures than juveniles.

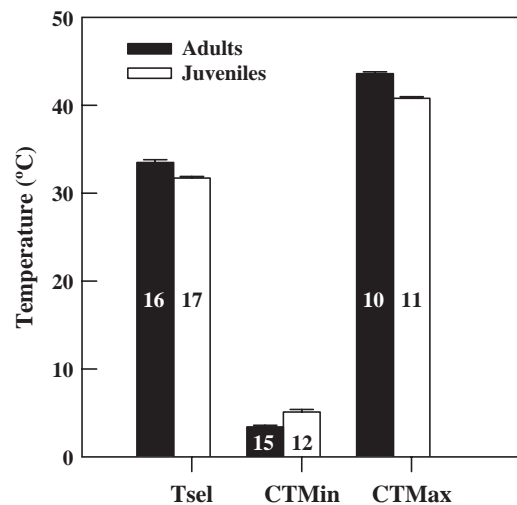


Fig. 1. Selected body temperature and the lower (CT_{min}) and upper (CT_{max}) limits of thermal tolerance of *E. brenchleyi*. Data are expressed as mean \pm SE, and numbers in bars are sample sizes.

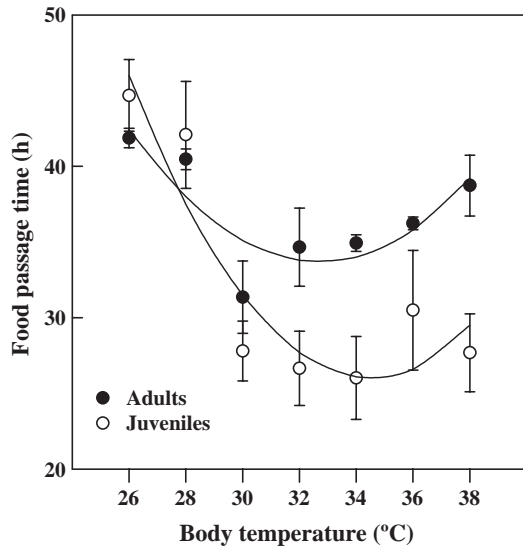


Fig. 2. Food passage time of *E. brechleyi* as a function of body temperature. Data are expressed as mean \pm SE. Ten adults and 9 juveniles were used at each test temperature, and a given lizard was used only at one test temperature. The curves were generated from a negative exponential fit on the original data.

3.2. Passage time, food intake, and food assimilation

Within each temperature treatment individual variation in all examined traits was evident but, except for final body mass, none of the traits was correlated with initial body size (mass) (all $P > 0.05$). Food passage time was affected by body temperature (two-way ANOVA, $F_{6,119} = 6.68$, $P < 0.0001$), and it was overall longer in adults than in juveniles (two-way ANOVA, $F_{1,119} = 20.61$, $P < 0.0001$). The effect of temperature \times age interaction on food passage time was significant (two-way ANOVA, $F_{6,119} = 2.51$, $P = 0.025$). In adults, food passage time generally decreased with increase in body temperature within the range of 26–32 °C and then increased at even higher body temperatures; in juveniles, passage rate generally decreased

with increase in body temperature within the range of 26–34 °C and then increased at higher body temperatures (Fig. 2).

The effects of body temperature, age, and temperature \times age interaction on daily food intake (mass-specific) were all significant. Lizards at body temperatures higher than 30 °C overall ate more than did those at lower body temperatures, and adults overall ate more than did juveniles (Tables 1 and 2). When influence of variation in initial body mass was removed using ANCOVA, final body masses were overall greater in lower temperature treatments (26–30 °C) than in higher temperature treatments, but did not differ between adults and juveniles (Table 2). ADC and AE both varied among temperature treatments, but no clear patterns for these two variables emerged (Tables 1 and 2). At body temperatures higher than 26 °C, ADC and AE were apparently greater in adults than in juveniles (Table 1).

3.3. Locomotor performance

Within each temperature treatment sprint speed was not correlated with body size (or mass) in both juveniles and adults (all $P > 0.05$). A repeated measures ANOVA showed that the effects of age ($F_{1,17} = 51.02$, $P < 0.0001$) and body temperature ($F_{8,136} = 5.82$, $P < 0.0001$) on sprint speed were significant but the effect of their interaction was not ($F_{8,136} = 1.37$, $P = 0.214$). In adults, sprint speed increased with increase in body temperature within the range of 22–30 °C and then decreased at higher body temperatures; in juveniles, sprint speed increased with increase in body temperature within the range of 22–34 °C, and then decreased at higher body temperatures (Fig. 3). At each test temperature sprint speeds were greater in adults than in juveniles (Fig. 3).

4. Discussion

Juvenile *E. brechleyi* selected lower body temperatures than adults, adding evidence for an ontogenetic shift in the set-point

Table 1
Changes in body mass, food intake, apparent digestive coefficient (ADC), and assimilation efficiency (AE) of *E. brechleyi* at different body temperatures

Body temperature (°C)	Juveniles (n=9)					Adults (n=10)				
	Initial body mass (g)	Final body mass (g)	Food intake (J. d ⁻¹ . g ⁻¹)	ADC (%)	AE (%)	Initial body mass (g)	Final body mass (g)	Food intake (J. d ⁻¹ . g ⁻¹)	ADC (%)	AE (%)
26	1.8 \pm 0.1 (1.3–2.1)	1.8 \pm 0.1 (1.4–2.2)	342.3 \pm 32.2 (206.9–537.2)	91.7 \pm 0.6 (89.1–95.4)	85.0 \pm 0.9 (81.9–89.6)	4.6 \pm 0.1 (4.0–5.7)	4.6 \pm 0.1 (4.1–5.4)	411.5 \pm 23.5 (273.4–477.7)	91.8 \pm 0.4 (89.9–93.3)	85.2 \pm 0.5 (83.1–87.4)
28	1.9 \pm 0.1 (1.4–2.5)	1.9 \pm 0.1 (1.3–2.5)	418.6 \pm 26.7 (296.1–583.2)	92.2 \pm 0.5 (89.0–95.0)	84.6 \pm 0.7 (81.5–88.2)	4.8 \pm 0.1 (4.1–5.8)	4.9 \pm 0.1 (4.3–5.9)	371.2 \pm 22.5 (289.7–521.0)	93.3 \pm 0.2 (92.5–94.2)	86.4 \pm 0.2 (85.9–87.7)
30	1.8 \pm 0.1 (1.3–2.2)	1.9 \pm 0.1 (1.5–2.1)	571.0 \pm 39.9 (453.7–806.6)	89.0 \pm 0.7 (85.3–91.6)	79.4 \pm 1.0 (72.8–83.5)	4.5 \pm 0.1 (3.8–5.0)	4.5 \pm 0.2 (3.7–5.2)	596.1 \pm 14.3 (515.5–674.3)	95.7 \pm 0.2 (94.8–96.8)	92.1 \pm 0.4 (90.4–94.5)
32	1.9 \pm 0.1 (1.5–2.1)	1.9 \pm 0.1 (1.4–2.2)	505.8 \pm 30.7 (356.0–685.4)	90.8 \pm 0.9 (82.2–94.0)	80.6 \pm 1.5 (66.2–86.6)	4.5 \pm 0.2 (3.8–5.5)	4.5 \pm 0.2 (3.7–5.5)	600.3 \pm 20.7 (463.4–684.2)	95.2 \pm 0.2 (94.1–95.9)	91.1 \pm 0.3 (88.7–92.0)
34	1.9 \pm 0.1 (1.4–2.4)	1.9 \pm 0.1 (1.5–2.3)	433.2 \pm 30.3 (293.3–578.9)	92.6 \pm 0.5 (89.3–95.9)	81.5 \pm 1.1 (75.7–87.4)	4.6 \pm 0.2 (3.9–5.5)	3.9 \pm 0.2 (3.0–5.1)	483.0 \pm 14.0 (417.9–546.6)	95.4 \pm 0.6 (90.9–97.9)	92.8 \pm 0.8 (87.6–96.4)
36	1.9 \pm 0.1 (1.5–2.1)	1.7 \pm 0.1 (1.4–1.9)	376.7 \pm 30.0 (242.9–539.1)	91.8 \pm 0.5 (88.1–95.5)	78.9 \pm 1.2 (69.8–83.3)	4.4 \pm 0.1 (3.9–5.2)	3.8 \pm 0.2 (3.0–4.7)	509.0 \pm 15.3 (441.9–586.4)	95.5 \pm 0.4 (93.6–96.9)	92.9 \pm 0.6 (89.6–92.7)
38	2.0 \pm 0.1 (1.6–2.4)	1.8 \pm 0.1 (1.3–2.0)	394.8 \pm 20.1 (272.7–514.4)	92.4 \pm 0.4 (90.0–95.5)	80.9 \pm 0.5 (78.6–83.9)	3.9 \pm 0.2 (3.2–5.0)	3.7 \pm 0.2 (3.1–5.2)	788.2 \pm 29.7 (609.3–929.9)	95.3 \pm 0.4 (92.8–96.7)	92.2 \pm 0.3 (90.5–93.5)

A given lizard was used only at one test temperature. Data are expressed as mean \pm SE (range).

Table 2
Results of two-way ANCOVA (for changes in body mass, with initial body mass as the covariate) and two-way ANOVA [for food intake, apparent digestive coefficient (ADC), and assimilation efficiency (AE)] with temperature and age as the factors

	Final body mass	Food intake	ADC	AE
Body temperature	$F_{6,118}=7.93, P<0.0001$ 26 ^a , 28 ^a , 30 ^a , 32 ^{ab} , 34 ^b , 36 ^b , 38 ^b	$F_{6,119}=25.78, P<0.0001$ 26 ^c , 28 ^{bc} , 30 ^a , 32 ^a , 34 ^b , 36 ^b , 38 ^a	$F_{6,119}=5.47, P<0.0001$ 26 ^b , 28 ^{ab} , 30 ^{ab} , 32 ^{ab} , 34 ^a , 36 ^a , 38 ^a	$F_{6,119}=2.76, P=0.015$ 26 ^b , 28 ^{ab} , 30 ^{ab} , 32 ^{ab} , 34 ^a , 36 ^{ab} , 38 ^{ab}
Age	$F_{1,118}=0.26, P=0.616$ adults=juveniles	$F_{1,119}=29.65, P<0.0001$ adults>juveniles	$F_{1,119}=118.48, P<0.0001$ adults>juveniles	$F_{1,119}=401.67, P<0.0001$ adults>juveniles
Body temperature × age interaction	$F_{6,118}=8.31, P<0.0001$	$F_{6,119}=15.19, P<0.0001$	$F_{6,119}=7.81, P<0.0001$	$F_{6,119}=23.50, P<0.0001$

Log_e (for food intake) or arcsine (for ADE and AE) transformations were performed prior to two-way ANOVA. Means corresponding to the temperature with different superscripts differed significantly (Tukey's test, $\alpha=0.05$, a>b>c).

of thermoregulation in lizards (Paulissen, 1988a). We are currently unaware whether this ontogenetic shift means that lizards of different age classes use different microhabitats due to the lack of field data. However, because final body masses (indicative of growth) were overall greater in lizards maintained at body temperatures from 26 to 30 °C (Table 2) and because growth could be ecologically more meaningful for juveniles than for adults, juveniles may certainly benefit more from selecting relatively lower body temperatures.

T_{sel} represents the body temperature at which numerous physiological and behavioral processes function at some optimal levels (Hutchison, 1976; Van Damme et al., 1991; Braña, 1993; Hertz et al., 1993; Christian and Weavers, 1996; Blouin-Demers et al., 2000; Angilletta et al., 2002). Previous studies using methodologies described in this study have shown that T_{sel} differs among lizards using different habitats. For example, lizards such as brown forest skinks (*Sphenomorphus indicus*; 25.7 °C, Ji et al., 1997) using shaded habitats select lower body temperatures, whereas those such as Chinese skinks (*Eumeces chinensis*; 31.2 °C, Ji et al., 1995) using open habitats select higher body temperatures. *Eremias brenchleyi* select higher body temperatures (33.5 °C for adults) than do northern grass lizards (*Takydromus septentrionalis*) (30.0 °C for adults, Ji et al.,

1996a) living in the same geographic region, mainly because the former species uses more opened habitats (Chen, 1991).

CT_{min} and CT_{max} also vary among and within reptilian species as a response to changes in thermal environments associated with habitat use or geographic variation in climate (Huey and Kingsolver, 1993; Bennett and Lenski, 1999; Feder et al., 2000; Angilletta et al., 2002; Winne and Keck, 2005). Overall, CT_{min} is higher in lizards using warmer habitats, and CT_{max} is higher in lizards living in open habitats (Zhang and Ji, 2004). Our data provide additional support for these two general conclusions. For example, CT_{min} is lower in adult *E. brenchleyi* (3.4 °C) than in adult *Takydromus sexlineatus* (southern grass lizard) (6.4 °C, Zhang and Ji, 2004) from warmer regions, and CT_{max} is higher in adult *E. brenchleyi* than in adult *T. septentrionalis* from the same region but living in more shaded habitats (Chen, 1991). Within the studied *E. brenchleyi* population, juveniles are less able to tolerate extreme body temperatures than adults, as our data showed a higher CT_{min} but a lower CT_{max} in juveniles (Table 1).

The ontogenetic shifts in T_{sel} , CT_{min} , and CT_{max} are of interest, because such shifts presumably imply that *E. brenchleyi* of different ages might, like other lizards that exhibit a non-random selection of microhabitats (Paulissen, 1988b; Melville and Schulte, 2001), use thermally different time or microhabitats to mitigate the juvenile–adult competition. Food habits of juveniles and adults differ considerably in *E. brenchleyi* (Xu and Ji, 2003). Because diel activity and habitat use may differ among different types of prey, it is plausible for juveniles to use different times or microhabitats with different thermal environments to maximize foraging success.

Currently, three patterns of temperature effects on food passage time have been reported for insectivorous lizards: (1) decreasing with increase in body temperature [*Uta stansburiana* (Waldschmidt et al., 1986); *T. septentrionalis* (Ji et al., 1996a)]; (2) decreasing with increase in body temperature at lower temperatures and leveling off at higher temperatures [*E. chinensis* (Ji et al., 1995); *S. indicus* (Ji et al., 1997); *T. wolteri* (Chen et al., 2003)]; (3) decreasing with increase in body temperature at lower temperatures and increasing at higher temperatures [*Lacerta vivipara* (Van Damme et al., 1991); *Sceloporus merriami* (Beaupre et al., 1993); *Eumeces elegans* (Du et al., 2000); *T. sexlineatus* (Zhang and Ji, 2004)]. These patterns are most probably true, because, at least for species studied in China (*E. chinensis*, *E. elegans*, *S. indicus*, *T.*

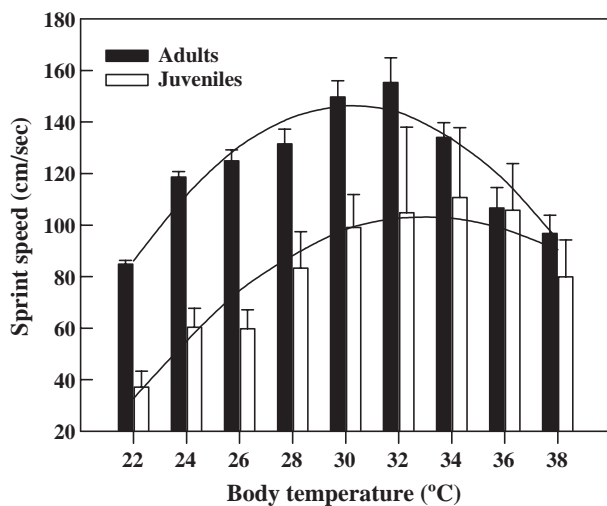


Fig. 3. Sprint speed of *E. brenchleyi* at different body temperatures. Data are expressed as mean±SE. Ten adults and 9 juveniles were used at each temperature, and individual lizards were used at all nine test temperatures. The curves were generated from a negative exponential fit on the original data.

septentrionalis, *T. sexlineatus*, and *T. wolteri*), the temperature range within which food passage time is determined is not only similar but also covers almost the whole range of body temperatures where feeding can occur. What is interesting is that these differences occur at the upper body temperatures, at which animals may not maintain for prolonged periods in nature. The thermal dependence of food passage time in *E. brenchleyi* seems to belong to Pattern 3 (Fig. 2). It is worth noting that food passage time was overall longer in adults than in juveniles, especially in lizards at body temperatures higher than 30 °C (Fig. 2).

The values of ADC and AE are determined by activities of digestive enzymes, food passage time, and type and amounts of food consumed (Andrews and Asato, 1977; Harwood, 1979; Beaupre et al., 1993; Witz and Lawrence, 1993; Zhang and Ji, 2004). Within a certain range, increased body temperature increases activities of digestive enzymes, but reduces the duration that food is exposed to these enzymes as food passage time is shortened (Harwood, 1979). It is this unique mechanism that results in thermal insensitivity of ADC and AE in all lizards studied so far (Dutton et al., 1975; Waldschmidt et al., 1986; Van Damme et al., 1991; Beaupre et al., 1993; Ji et al., 1993, 1995, 1996a, 1997; Xu et al., 1999; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004). In our study, juveniles and adults were both fed with mealworms of the same size that did not differ in composition (Ji et al., 1996b), but ADC and AE were overall greater in adults than in juveniles. We interpret these differences as partly due to the fact that food passage time was overall longer in adults (Fig. 1), because prolonged exposure of food to enzymatic action due to the increased food passage time can increase values of ADC and AE.

At each test body temperature the mean sprint speed was greater in adults. The range of body temperatures where lizards maintained 90% of maximum speed differed between adults (27–34 °C) and juveniles (29–37 °C) (Fig. 2). This finding is also interesting because it provides evidence for an ontogenetic shift in optimal body temperature for locomotor performance. Clearly, the optimal temperatures for growth are different from the optimal temperatures for locomotor performance in both juveniles and adults. Thus, selecting lower body temperatures to maximize growth may reduce locomotor capacities in *E. brenchleyi*.

Collectively, our results present clear evidence of ontogenetic shifts in thermal tolerance, selected body temperature, and thermal dependence of food assimilation and locomotor performance in *E. brenchleyi*. Our results show also that thermal optima and thermal sensitivities differ between food assimilation and sprint speed and, thus, add support for the multiple optima hypothesis for the thermal dependence of behavioral and physiological performance in reptiles (Huey, 1982; Angilletta et al., 2002).

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