

## Thermal dependence of food assimilation and sprint speed in a lacertid lizard *Eremias argus* from northern China \*

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**Abstract** We collected adult *Eremias argus* (Lacertidae) from a population in Yangquan (Shanxi, northern China) to study thermal dependence of food assimilation and sprint speed. Selected body temperature (T<sub>sel</sub>) measured on a laboratory thermal gradient was 36.0°C; critical thermal minimum (CT<sub>Min</sub>) and critical thermal maximum (CT<sub>Max</sub>) averaged 1.0°C and 44.9°C, respectively. Differences in T<sub>sel</sub>, CT<sub>Min</sub> and CT<sub>Max</sub> were not found between-sex. Within the range of body temperatures considered, food passage time, daily food intake, daily production of feces and urates, apparent digestive coefficient (ADC) and assimilation efficiency (AE) were all affected by body temperature. Food passage time decreased with increase in body temperature within the range from 26°C to 34°C, and then increased at higher body temperatures. Lizards at 30, 32, 34 and 36°C ate more food and produced more feces and urates than did those at 28°C and 38°C. Although ADC and AE were both higher at 34°C and 36°C than at other lower or higher temperatures, no clear patterns associated with temperature could be discerned for these two variables. Sprint speed increased with increase in body temperature within the range from 18°C to 36°C, and then decreased at 38°C. The body temperatures maximizing sprint speed was around 36°C, which was much close to the mean value of body temperatures selected by lizards on the thermal gradient. This result adds evidence that the range of optimal body temperatures for sprint speed is tightly coupled with T<sub>sel</sub> in lizards [*Acta Zoologica Sinica* 52 (2): 256–262, 2006].

**Key words** Reptilia, Lacertidae, *Eremias argus*, Selected body temperature, Thermal tolerance, Sprint speed, Food assimilation

## 华北丽斑麻蜥食物同化和疾跑速的热依赖性 \*

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**摘要** 作者研究山西阳泉丽斑麻蜥 (*Eremias argus*) 成体的选择体温、热耐受性及食物同化和疾跑速的热依赖性。选择体温、临界低温和临界高温无显著的两性差异, 分别为 36.0°C、1.0°C 和 44.9°C。在实验温度范围内, 体温显著影响食物通过时间、日摄食量、日粪尿排量、表观消化系数和同化效率。食物通过时间在 26–34°C 范围内随体温升高而缩短, 在更高的体温下则延长。蜥蜴在 30、32、34 和 36°C 体温下明显摄入较多的食物、排出明显较多的粪尿。34°C 和 36°C 下的表观消化系数和同化效率大于其它更低或更高温度下的对应数值, 但这两个变量未因体温变化而呈现清晰的规律性变化。疾跑速在 18–36°C 范围内随体温升高而加快, 在 38°C 体温下则减缓。36°C 或附近体温最适合疾跑速。疾跑速最适体温接近蜥蜴的选择体温, 表明蜥蜴疾跑速的最适温度可能与其选择体温密切相关 [*动物学报* 52 (2): 256–262, 2006]。

**关键词** 爬行纲 蜥蜴科 丽斑麻蜥 选择体温 热耐受性 疾跑速 食物同化

Reptiles can regulate body temperature by behavioral mechanisms when temporally and spatially variable heat sources are available to them, thereby

maintaining relatively high and constant body temperatures so that physiological and behavioral performances can be expressed at relatively high levels

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(Cowles and Bogert, 1944; Bartholomew, 1977). In uniform thermal environments such as underground, underwater, and deeply shaded forests, variation in body temperature typically tracks variation in ambient temperature, because behavioral thermoregulation is constrained. Such constraints are particularly severe for reptiles in which physiological thermoregulation is very limited or even negligible (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 an individual's body temperatures can be controlled so that the upper and lower limits of thermal tolerance and functional capabilities at any given body temperature can be examined. Data from laboratory studies have showed 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, 1996; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004). Moreover, inter-specific comparisons reveal that reptiles living in different habitats and geographic or climatic regions often differ in thermal tolerance and select different body temperatures (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; see also Angilletta, 2001).

Most studies on thermal dependence of behavioral and physiological capacities in reptiles have focused on thermal dependence of food assimilation and locomotor performance. This may be not only because these two ecologically relevant variables can be easily measured but also because they are both associated with an individual's fitness. For example, net energy gains achieved by feeding can be translated into somatic tissue growth and/or production of offspring (Nagy, 1983), whereas locomotor performance is important for avoiding predators and enhancing foraging success (Pough, 1989; Bauwens et al., 1995; Miles et al., 1995; Shine, 2003). Available data in this field show that no specific temperature can maximize all physiological and behavioral capacities (e.g., Bustard, 1967; Lang, 1979; Pough, 1980; Huey, 1982; see also Angilletta et al., 2002) and that the thermal optima and thermal sensitivities differ between food assimilation and locomotor performance in nearly all reptilian species studied to date (e.g., Van Damme et al., 1991; Ji et al., 1995, 1996; Du et al., 2000; Xu et al., 2001; Chen et al., 2003; Zhang and Ji, 2004).

Here, we present data on selected body tempera-

ture, thermal tolerance and thermal dependence of food assimilation and locomotor performance collected in *Eremias argus*. Our aims are: (1) to provide data on a lizard whose thermal biology is completely unknown; (2) to compare data collected in this study with those reported for other species of lizards; and (3) to discuss how some of the inter-specific differences may be adaptive to the different habitat or climatic conditions faced by each species.

## 1 Materials and methods

### 1.1 Collection and animal care

*Eremias argus* is a small [up to 62 mm snout-vent length (SVL)] oviparous lacertid lizard, with a distributional range covering the northern provinces of China, Korea, Mongolia and Russia (Irkutsk), and lizards have been reported to use open habitats in plain and hilly countryside (Zhao, 1999). Adult lizards were collected in early April of 2003 and 2004 from a population in Shanxi, and were transported to our laboratory in Hangzhou, where each was sexed, weighed, and measured for SVL. Prior to the experiment and during intervals of trials, lizards were maintained ten to each 50 cm × 40 cm × 50 cm glass cage of which the bottom was filled with moist soil, grasses and pieces of clay tiles. These cages were placed in a room where temperatures were never higher than 28°C. A 100-W light bulb, suspended at one end of each cage, created a thermal gradient from room temperatures to 55°C for 12 h daily. Lizards were exposed to a natural daylight cycle and some direct sunlight, and could regulate body temperature behaviorally during the photophase. Lizards were fed mealworms *Tenebrio molitor* and water enriched with vitamins and minerals *ad libitum*.

### 1.2 Selected body temperature and thermal tolerance

A total of 21 lizards (9 females and 12 males) were used in the Tsel (selected body temperature) experiment, and another sample of 21 lizards (13 females and 8 males) was used in the CTMin (critical thermal minimum) and CTMax (critical thermal maximum) experiments. We first conducted the CTMin experiment and then (one week later) the CTMax experiment. Prior to each experiment, lizards were maintained at 28°C for 48 h to habituate to the starting temperature.

The Tsel experiment was conducted in a 100 cm × 50 cm × 45 cm glass cage covered with moist soil, grasses and pieces of clay tiles. Two light bulbs (total 500 W) suspended above one end created a thermal gradient ranging from room temperature to 60°C for 12 h daily, and lights were switched on at 07:00 h. Lizards were initially moved into the cage from the cool side at 09:00 h and, 24 h later, they were mea-

sured for body temperature (cloacal,  $T_b$ ) at 09:00, 12:00 and 15:00 h using an electronic thermometer, which had an external thermal probe and was previously calibrated with a standard thermometer. This thermometer allowed us to make the measures as fast as possible, thereby avoiding heat transfer occurring between hands and the measuring lizard.

We determined CTMin and CTMax by using an incubator (Ningbo Life Co., China). Both experiments were conducted during 10:00–15:00 h. We cooled (the CTMin experiment) or heated (the CTMax experiment) lizards from 28°C at the rate of 0.25°C/min and more slowly (0.1°C/min) when temperatures inside the incubator were lower than 8°C or higher than 38°C. During the experiments, we observed the behavior of the lizards through the glass door of the incubator. Body temperatures associated with a transient loss of the righting response (lizards could not reverse when they were turned over) at the lower and the upper limits were considered to be the endpoints for CTMin and CTMax, respectively (Ji et al., 1995). Three females and two males died in three days following the CTMax experiment, probably because they were over heated during the experiment. Data for these lizards were excluded from statistical analysis, because their values of CTMax were different from others.

### 1.3 Food passage time, food intake, and food assimilation

A total of 49 lizards (7 lizards at each temperature) were randomly assigned to seven constant temperature rooms, where their body temperatures could be controlled constant at 26, 28, 30, 32, 34, 36, and 38 ( $\pm 0.5$ )°C, respectively. We fixed the lower body temperature at 26°C, because lizards at temperatures lower than 26°C refused to eat. The fluorescent tubes in the constant temperature rooms were on a 12L:12D cycle, and the photophase started at 07:00 h. Lizards were housed individually in 25 cm  $\times$  15 cm  $\times$  25 cm glass terraria. We fasted lizards at the test temperature for 3 days prior to feeding, and then fed each lizard two mealworms marked individually by inserting a 2-mm red plastic thread (diameter 0.2 mm) into the larvae's body, which was used as a marker to estimate food passage time. We allowed lizards to eat the marked mealworms voluntarily, thereby avoiding 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 collecting the marked plastic threads in time. Mealworms assigned to each lizard were weighted prior to feeding, and those remaining at the end of the experiment were weighed again so that food intake could be determined.

Food passage time was defined as the time interval 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 accurate calorimetry. The initial body mass were recorded at the end of 3-d fast prior to feeding, and the final body mass was measured following another 3-d fast at the end of each trial.

Feces, urates, and the remaining mealworms corresponding to each lizard were dried to constant mass at 65°C and weighed. Dried samples were burned in a WZR-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).

### 1.4 Sprint speed

An independent sample of 10 lizards was measured for sprint speed at eleven body temperatures ranging from 18 to 38 ( $\pm 0.5$ )°C. Each lizard was used at all the eleven temperatures. The sequence of temperature was randomized over time. We placed lizards in an incubator for at least 2 h and then checked their body temperatures prior to each trial, thereby insuring their body temperatures to be controlled at the test level. Lizards were chased with a paintbrush down the length of a 150 cm  $\times$  10 cm  $\times$  15 cm wood racetrack with one side transparent, which allows lateral filmation with a digital video camera. Each lizard was sprinted twice at each temperature with a minimum of 30 min rest between the two trials, and was given 24 h to rest between temperatures. The tapes were later read out with a computer using MGI Video Wave III software (MGI Software Co., Canada) for sprint speed in the fastest 25 cm interval.

### 1.5 Statistical analyses

A preliminary analysis revealed no between-sex differences in the examined traits, so we pooled data for both sexes. All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances ( $F$ -max test), and  $\log_e$  transformations were performed when necessary to satisfy the assumptions for parametric analyses. One-way ANOVA (for food passage time and daily food intake), one-way ANCOVA (for final body mass using initial body mass as the covariate, and ADC and AE using food intake as the covariate) and repeated measures ANOVA (for sprint speed with the body temperature as the within-subject factor) were used to analyze data. Descriptive statistics were presented as mean  $\pm 1$  standard error, and the significance level was set at  $\alpha = 0.05$ .

## 2 Result

Lizards at 09:00, 12:00 and 15:00 h did not select different body temperatures (repeated measures ANOVA,  $F_{2, 38} = 0.415$ ,  $P = 0.663$ ), so we pooled data for each lizard. Body temperatures selected by lizards ( $n = 21$ ) varied from 32.8°C to 38.5°C, with the mean (indicative of Tsel; Ji et al., 1995) being 36.0°C and the median 36.1°C. The central 80% of all selected temperature readings, an estimate of the preference zone for behavioral thermoregulation (Bauwens et al., 1995), included the values within the range from 34.3°C to 38.0°C. CTMin varied from -0.3°C to 2.4°C (Mean = 1.0°C,  $n = 21$ ), and CTMax from 43.2°C to 47.6°C (Mean = 44.9°C,  $n = 16$ ).

Body temperature affected food passage time

(ANOVA,  $F_{6, 42} = 468.12$ ,  $P < 0.001$ ), which decreased with increased in body temperature within the range from 26°C to 34°C and then increased at higher temperatures (Fig. 1). Lizards used to examine thermal dependence of food assimilation did not differ among temperature treatments in SVL and initial body mass (ANOVA, both  $P > 0.49$ ) but in daily food intake, daily production of feces and daily reproduction of urates (ANOVA, all  $P < 0.004$ ). Lizards at 30, 32, 34, and 36°C ate more food and produced more feces and urates than did those at other two temperatures (Table 1). Both ADC (ANCOVA,  $F_{5, 35} = 17.35$ ,  $P < 0.0001$ ) and AE (ANCOVA,  $F_{5, 35} = 9.82$ ,  $P < 0.0001$ ) varied among temperature treatments, with the two variables being both greater at 34°C and 36°C than at other lower or higher temperatures (Table 1).

**Table 1 Initial body mass, daily food intake, daily reproduction of faeces, daily production of urates, apparent digestive coefficient (ADC) and assimilation efficiency (AE) of adult *Eremias argus* ( $n = 42$ , 7 lizards to each temperature)**

Body temperature (°C)	Initial body mass (g)	Daily food intake ( $J \cdot d^{-1} \cdot g^{-1}$ )	Daily production of feces ( $J \cdot d^{-1} \cdot g^{-1}$ )	Daily production of urates ( $J \cdot d^{-1} \cdot g^{-1}$ )	ADC (%)	AE (%)
28	3.9 ± 0.1 (3.6–4.4)	233.7 <sup>d</sup> ± 15.1 (195.9–279.0)	20.8 <sup>b</sup> ± 1.6 (13.4–26.4)	20.7 <sup>b</sup> ± 1.5 (15.4–25.0)	91.1 <sup>bc</sup> ± 0.5 (89.7–93.3)	82.2 <sup>bc</sup> ± 0.9 (78.2–85.2)
30	3.6 ± 0.2 (2.8–4.1)	324.2 <sup>bc</sup> ± 14.4 (311.5–420.9)	34.1 <sup>a</sup> ± 1.4 (31.0–41.3)	28.0 <sup>ab</sup> ± 1.3 (25.0–34.8)	90.0 <sup>cd</sup> ± 0.2 (89.4–91.3)	81.8 <sup>bc</sup> ± 0.3 (80.9–83.7)
32	3.7 ± 0.1 (3.4–4.2)	381.0 <sup>ab</sup> ± 20.8 (318.0–459.4)	42.7 <sup>a</sup> ± 3.2 (34.9–56.5)	31.4 <sup>a</sup> ± 1.70 (22.7–36.2)	88.7 <sup>d</sup> ± 0.8 (84.9–91.0)	80.4 <sup>c</sup> ± 0.7 (78.3–83.1)
34	3.9 ± 0.1 (3.7–4.3)	440.7 <sup>a</sup> ± 21.4 (380.9–504.9)	23.0 <sup>b</sup> ± 3.6 (13.4–41.4)	30.0 <sup>ab</sup> ± 4.7 (18.9–52.4)	94.9 <sup>a</sup> ± 0.6 (91.7–96.6)	88.2 <sup>a</sup> ± 1.4 (81.3–91.6)
36	3.9 ± 0.2 (3.3–4.7)	359.18 <sup>bc</sup> ± 24.5 (295.4–473.1)	23.2 <sup>b</sup> ± 2.4 (16.0–34.5)	22.3 <sup>ab</sup> ± 1.3 (18.7–27.9)	93.5 <sup>ab</sup> ± 0.5 (91.6–95.7)	87.2 <sup>a</sup> ± 0.8 (84.7–90.5)
38	4.0 ± 0.2 (3.1–4.5)	281.5 <sup>cd</sup> ± 15.2 (230.0–334.1)	23.2 <sup>b</sup> ± 1.5 (18.2–29.6)	20.5 <sup>b</sup> ± 1.9 (15.0–27.6)	91.7 <sup>bc</sup> ± 0.5 (90.2–93.8)	84.5 <sup>b</sup> ± 1.0 (80.4–88.6)

Data are expressed as mean ± 1 standard error (range). Means with different lettered superscripts differ significantly (Tukey's test,  $\alpha = 0.05$ ;  $a > b > c > d$ ). See text for detailed statistical results.

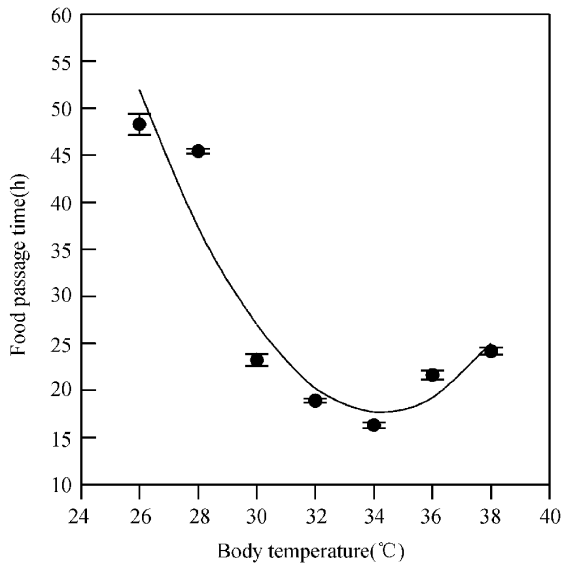
Body temperature affected sprint speed (repeated measures ANOVA,  $F_{10, 90} = 13.30$ ,  $P < 0.00001$ ), which increased with increase in body temperature within the range from 18°C to 36°C (Fig. 2). Statistically speaking, the range of optimal body temperatures for sprint speed was somewhere between 28°C and 38°C, with sprint speed being maximized at 36°C (Fig. 2).

## 3 Discussion

Selected body temperature represents the body temperature at which numerous processes can 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 show that Tsel may differ among lizards using

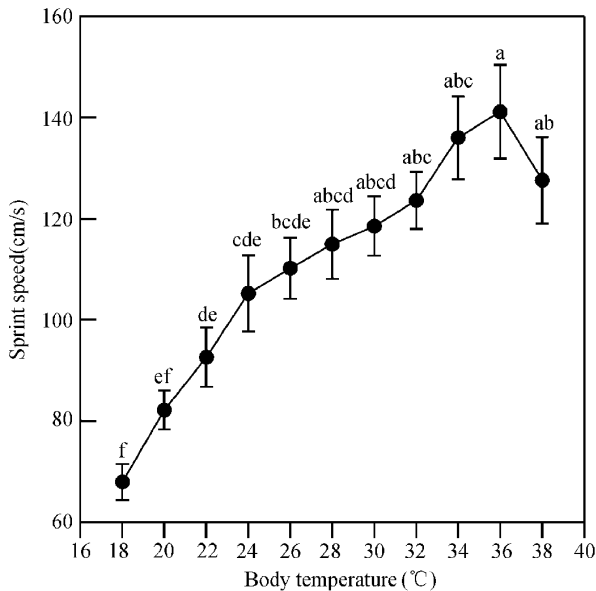
different habitats or living in different geographic or climatic regions. For example, lizards such as brown forest skinks *Sphenomorphus indicus* select relatively low body temperatures (25.7°C), primarily because they use forestry habitats, where ambient temperatures are rarely higher than 30°C (Ji et al., 1997). On the contrary, lizards using more opened habitats such as Chinese skinks (*Eumeces chinensis*: Ji et al., 1995), blue-tailed skinks (*E. elegans*: Du et al., 2000), upland racerunners (*Eremias brenchleyi*: Xu et al., 2001) and northern grass lizards (*Takydromus septentrionalis*: Ji et al., 1996) select body temperatures averagely at 31.2, 30.4, 33.7 and 30.0°C, respectively. Lizards of *E. argus* select relatively high body temperatures, presumably because they use open space in nature (Zhao, 1999).

The values of CTMin and CTMax reflect an



**Fig. 1** Food passage time ( $n = 49$ , 7 lizards to each temperature) of *Eremias argus* as a function of body temperature

Data are expressed as mean  $\pm$  1 standard error. The curve is generated from a negative exponential fit on the original data.



**Fig. 2** Sprint speed of *Eremias argus* ( $n = 10$ ) at different body temperatures

Data are expressed as mean  $\pm$  1 standard error. Each lizard was used at all eleven test temperatures. Means with different superscripts differ significantly (Tukey's test,  $\alpha = 0.05$ ;  $a > b > c > d > e > f$ ).

adaptation to the thermal environments experienced by lizards in nature, and may vary considerably among species differing in habitat use or geographic distribution (Huey and Kingsolver, 1993; Bennett and Lanski, 1999; Feder et al., 2000; Angilletta et al., 2002; Winne and Keck, 2005). Overall, CT<sub>Min</sub> is higher in lizards using more opened habitats or

living in warmer regions, and CT<sub>Max</sub> is higher in lizards using more opened habitats where ambient temperatures often fluctuate considerably (Zhang and Ji, 2004). For example, *E. argus* can tolerate a wider range of temperatures (1.0 – 44.9°C) than *E. brenchleyi* (3.4 – 43.6°C; Xu et al., 2001), presumably because the former species is distributed in more northerly regions where ambient temperatures fluctuate more considerably than the regions occupied by the latter species (Zhao, 1999).

Three patterns of the thermal dependence of food passage time have been identified in lizards: (1) decreasing with increase in body temperature (*Uta stansburiana*: Waldschmidt et al., 1986; *T. septentrionalis*: Ji et al., 1996; *Sceloporus undulatus*: Angilletta, 2001); (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; *Takydromus wolteri*: Chen et al., 2003); and (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; *E. brenchleyi*: Xu et al., 2001; *Takydromus sexlineatus*: Zhang and Ji, 2004). As in *E. brenchleyi* (a congeneric species), the thermal dependence of passage time seems to belong to Pattern 3 in *E. argus* (Fig. 1).

The values of ADC and AE are influenced by activities of digestive enzymes, food passage time, food type and amounts of food consumed (Andrews and Asato, 1977; Harwood, 1979; Beaupre et al., 1993; Witz and Lawrence, 1993; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004). Within a certain range, increased body temperature increases activities of digestive enzymes but reduces the food passage time (Harwood, 1979). It is this unique mechanism that makes ADC and AE thermally less sensitive in nearly all species of lizards studied to date. In this study, ADC and AE both varied among temperature treatments. ADC and AE were both greater at 34°C and 36°C than at other lower or higher temperatures, but no clear patterns associated with temperature could be discerned for these two variables (Table 1). For example, both ADC and AE were lower at 32°C than at other lower or higher temperatures for some unknown reasons. The values of ADC and AE at other temperatures were actually very close (Table 1), suggesting that *E. argus* is still among the species in which both traits are less sensitive to variation in body temperature.

As in numerous other lizards (Bennett, 1980; Van Damme et al., 1991; Ji et al., 1995; Du et al., 2000; Xu et al., 2001; Chen et al., 2003; Zhang et

al., 2004), inter-individual differences in sprint speed are very pronounced in *E. argus* (Fig.2). The range of optimal body temperatures for sprint speed in *E. argus* was somewhere between 28°C and 38°C. This range is higher than the values (30–34°C) reported for other species of lizards, including *E. chinensis* (Ji et al., 1995), *E. elegans* (Du et al., 2000), *E. brenchleyi* (Xu et al., 2001), *T. sexlineatus* (Zhang et al., 2004), *T. septentrionalis* (Ji et al., 1996) and *T. wolteri* (Chen et al., 2003). Interestingly, the temperature that maximizes sprint speed of *E. argus* is much close to the mean value of body temperatures selected by lizards on the thermal gradient. This result presumably suggests that the range of optimal body temperatures for sprint speed is tightly coupled with  $T_{sel}$  in lizards.

Unlike other lizards for which we have data, the temperatures maximizing sprint speed also maximize ADC and AE in *E. argus* (Table 1, Fig.2). Most probably, this consistency of the thermal optima explains why *E. argus* maintain a higher body temperature.

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