

Thermal preference, thermal tolerance and the thermal dependence of digestive performance in two *Phrynocephalus* lizards (Agamidae), with a review of species studied

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Abstract We reported data on thermal preference, thermal tolerance and the thermal dependence of digestive performance for two *Phrynocephalus* lizards (*P. frontalis* and *P. versicolor*), and compared data among lizards so far studied worldwide. Mean values for selected body temperature (Tsel) and critical thermal maximum (CTMax) were greater in *P. versicolor*, whereas mean values for critical thermal minimum (CTMin) did not differ between the two species. The two lizards differed in food intake, but not in food passage time, apparent digestive coefficient (ADC) and assimilation efficiency (AE), across the experimental temperatures. Four general conclusions can be drawn from published data. Firstly, thermal preference and thermal tolerance differ among lizards differing in distribution, temporal activity pattern and habitat use. Lizards in thermally more variable regions are better able to tolerate low and high temperatures. Diurnal lizards generally select higher body temperatures than nocturnal lizards, and lizards using habitats with direct sun exposure generally selected higher body temperatures and are better able to tolerate high temperatures. Secondly, CTMax is positively correlated with Tsel. Lizards more likely exposed to extremely high temperatures while active select higher body temperatures than those using shaded habitats. Thirdly, the effects of body temperature on food intake, food passage time, ADC and AE differ among lizards, but it seems to be common among lizards that ADC and AE are less thermally sensitive than food intake and food passage time. Lastly, ADC is dependent on the type of food ingested, with insectivorous lizards digesting food more efficiently than herbivorous lizards [*Current Zoology* 57 (6): 684–700, 2011].

Keywords Lizards, Selected body temperature, Critical thermal limits, Food intake, Food passage time, Apparent digestive coefficient, Assimilation efficiency

Temperature influences many biological processes in organisms and has consequences on their habitat requirements and hence spatial distribution (Tinkle and Gibbons, 1977; Angilletta et al., 2002b; Edwards and Richardson, 2004; Helland et al., 2007; Martin and Huey, 2008). It has been suggested that temperature is a part of an organism's multidimensional niche and should be treated as an ecological resource (Magnuson et al., 1979; Cerda et al., 1998). In ectotherms, environmental temperature influences body temperature, which in turn, affects physiological processes and behavioral performances that are linked to these processes (Angilletta et al., 2002b). Extremely low or high body temperatures are harmful and even lethal to organisms, whereas moderate to relatively high body temperatures often maximize functional capacities (Huey, 1982; Huey

and Kingsolver, 1989; Navas et al., 1999; Angilletta et al., 2002b). It is therefore not surprising that diverse ectotherms attempt to maintain relatively high and constant temperatures while active. Ectotherms heavily rely on behavioral mechanisms such as basking intensity, restriction of activity periods and selective exploitation of environmental thermal flux to regulate body temperature (Avery, 1982; Bartholomew, 1982; Huey, 1982). The upper (critical thermal maximum, CTMax) and lower (critical thermal minimum, CTMin) thermal limits can be estimated by measuring the body temperatures associated with the loss of righting response at the upper and lower thermal limits (Lutterschmidt and Hutchison, 1997), and the body temperature preferred by an ectotherm can be estimated by measuring its selected body temperature (Tsel) in a laboratory thermal

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gradient (Angilletta et al., 2002b).

Thermal preference and thermal tolerance have been examined in diverse animal taxa, and lizards are among the most extensively studied taxa (Appendix 1). Thermal preference and thermal tolerance differ among lizard species that differ in habitat use (open *versus* shaded habitats, or warm *versus* cool habitats), temporal activity pattern (diurnally-*versus* nocturnally-active species), and geographic distribution (Huey et al., 1989; Andrews, 1998; Feder et al., 2000; Melville and Schulte, 2001; Winne and Keck, 2005), and among lizards of the same population that differ in physiological, or developmental conditions (Mathies and Andrews, 1997; Le Galliard et al., 2003; Xu and Ji, 2006; Lin et al., 2008). For example, lizards using cooler habitats select lower body temperatures and show a greater resistance to low temperatures than those of the same local community using warmer habitats (Ji et al., 1997; Du et al., 2006), lizards often shift their thermal preferences upwards after feeding to facilitate digestion and absorption (Huey, 1982; Sievert, 1989; Brown and Griffin, 2005; Ding et al., 2007; Li et al., 2010), and females often shift their thermal preferences downwards or upwards when pregnant to provide optimal temperatures for their embryos (Braña, 1993; Mathies and Andrews, 1997; Le Galliard et al., 2003; Ji et al., 2007; Yan et al., 2011). Ontogenetic shifts in thermal preference and thermal tolerance have been detected in several lizard species (Paulissen, 1988; Xu et al., 1999; Melville and Schulte, 2001; Xu and Ji, 2006; Qiu et al., 2009; Shu et al., 2010a), and such shifts may have an implication for a non-random selection of habitats that allows lizards of different ages to use thermally different habitats and thereby reduce the juvenile-adult competition.

Digestive efficiencies [apparent digestive coefficient (ADC) and assimilation efficiency (AE)] are associated with an individual's fitness, because net energy gains achieved from feeding can be allocated to somatic growth and production of offspring (Nagy, 1983; Bedford and Christian, 2000; Pafilis et al., 2007; Luo et al., 2010). The effects of body temperature on ADC and AE have been examined in diverse lizard taxa (Appendix 2). Previous studies show that ADC and AE are influenced by many factors such as enzymatic activity, food passage time and the type and amount of food ingested (Andrews and Asato, 1977; Harwood, 1979; Beaupre et al., 1993; Witz and Lawrence, 1993; Pafilis et al., 2007). Increasing body temperature increases enzymatic activity but reduces exposure of food to enzymatic action due to the shortened food passage time. This unique

mechanism makes ADC and AE less thermally sensitive than other measures of digestive performance such as food intake and food passage time (Xu and Ji, 2006). Often can one find that ADC and AE are less variable over a wide range of body temperatures, or reduce at temperatures close to the lower and/or upper thresholds over which feeding cannot occur (Ji et al., 1995; Zhang and Ji, 2004; Luo et al., 2006; Xu and Ji, 2006; Li et al., 2009b).

Here, we present data on thermal preference, thermal tolerance and the thermal dependence of digestive performance collected in two oviparous toad-headed lizards of the genus *Phrynocephalus*, *P. frontalis* and *P. versicolor*. Toad-headed lizards as a whole are widely distributed in arid or semiarid areas in Central and West Asia, westward to South Jordan and eastwards to Hebei Province of China, with *P. frontalis* having the most easterly distribution (Zhao, 1999). Widespread sympatry between different species pairs occurs in several areas of China, such as *P. frontalis* and *P. versicolor* in central Inner Mongolia, *P. przewalskii* and *P. versicolor* in western Inner Mongolia, *P. axillaris* and *P. forsythii* in southern Xinjiang, and *P. putjatia* and *P. vlangaii* in eastern Qinghai (Zhao, 1999; Nobel et al., 2010), but little is known about why and how these co-occurring species exist in their sympatric areas. Lizards in this study were collected in the central part of Inner Mongolia, where the two species are sympatric, or syntopic. We address two questions: (1) Do the two species differ in thermal preference, thermal tolerance and the thermal dependence of digestive performance? (2) If so, are differences in particular measures indicative of differences in habitat use between the two species in the sympatric area? We compared data among lizards so far studied worldwide, aiming to draw some general conclusions.

1 Materials and Methods

1.1 Animal collection and care

We collected adult lizards (> 44 mm snout-vent length) in early May 2005 in an area between Ordos (40°02'N, 107°01'E) and Wulatehouqi (41°27'N, 106°59'E), Inner Mongolia. The annual mean temperature in this area varies from approximately 8–9 °C, and the annual rainfall from approximately 130–320 mm (courtesy of the Department of Meteorology of Inner Mongolia). Lizards were brought to our laboratory in Nanjing. Prior to the experiment and during trial intervals, between 10–15 individuals were housed in each 1 × 0.6 × 0.4 m (length × width × height) communal cage, in an indoor animal holding facility. The communal

cages contained a substrate of sand (~150 mm depth), with rocks and pieces of clay tiles provided as shelter and basking sites. Thermoregulatory opportunities were provided during daylight hours (05:00–19:00 h) by two 100-W incandescent lamps suspended over one end of the cage; overnight temperatures followed indoor air temperatures (23–28 °C). Lizards were provided with mealworms (*Tenebrio molitor*) and water enriched with vitamins and minerals *ad libitum*.

1.2 Thermal preference and thermal tolerance

Twenty adult *P. frontalis* and 20 adult *P. versicolor*, 10 females and 10 males for each species, were used in the experiment conducted in August 2005, about one month after the breeding season (from late May to early July; Qu et al., 2011a). Lizards were fasted for one day before testing. The experimental sequence was Tsel, CTMin and CTMax, at one-week intervals to minimize possible interactions between trials. No formal thermal acclimation was employed, but lizards of the two species had been maintained under the identical conditions described above for more than three months before they were measured.

We measured Tsel in a 1 × 0.8 × 0.4 m glass terrarium covered with sand and pieces of clay tiles. Two 150-W light bulbs suspended above one end created a thermal gradient ranging from the room temperature to 60 °C for 12 h daily, and lights were switched on at 07:00 h. Lizards were individually moved from the cool side into the terrarium at 10:00 h, and were measured for body temperature (cloacal, Tb) between 16:00–18:00 h using a UT-325 electronic thermometer (Shanghai Medical Instruments, China), which had an external thermal probe (1 mm diameter) and was previously calibrated with a standard mercury thermometer (Yun-run Instruments, China). We measured each lizard twice, once on each of two consecutive days. The two measures did not differ significantly (paired-sample *t*-test; *P* > 0.35 in all cases), so we considered the mean of the two measures as an individual's Tsel.

CTMin and CTMax were determined by using FPQ incubators (Ningbo Life Instruments, China). Trials were conducted during 13:00–16:00 h. We cooled (for the CTMin determination) or heated (for the CTMax determination) lizards from 28 °C at the rate of 0.25 °C min⁻¹ and more slowly (0.1 °C min⁻¹) when temperatures inside the incubator were lower than 5 °C or higher than 40 °C. During the trials, we observed the behavior of the lizards through a window in the incubator door. Body temperatures associated with a transient

loss of the righting response (lizards did not respond to intense stimulation and could not turn back when they were turned over) at the lower and the upper limits of the thermal tolerance were considered as the endpoints for CTMin and CTMax, respectively. All lizards recovered after testing, and none of them died in the following two months.

1.3 Food passage time, food intake and food assimilation

The experiment was conducted in September 2005. We used a repeated-measures experimental design to determine the effect of body temperature on food passage time. Eighteen adult males, nine for each species, were used at all test temperatures ranging from 24 °C to 40 °C. Trials were conducted in an a 3 × 4 m AAPS (artificial atmospheric phenomena simulator) room, and the sequence was randomized across temperatures (34, 26, 40, 24, 38 and 32 °C). We individually housed lizards in 200 × 200 × 200 mm glass cages, fasted them for 3 d prior to feeding, and then allowed each lizard to eat two mealworms marked with a 3-mm red plastic thread (0.2 mm diameter) inserted into the abdomen. Plastic threads were always collected within a few minutes after being expelled, and food passage time was defined as the lapsed time from swallowing to appearance of the first plastic thread.

Another independent sample of 58 adult males of *P. frontalis* and 59 adult males of *P. versicolor* was used to examine the thermal dependence of food intake and food assimilation. Lizards were moved into three AAPS rooms, where their body temperatures were controlled constant at 25, 33 and 39 (±0.5) °C, respectively. The temperature of 33 °C was within the range of body temperatures selected by the two species, more close to the mean Tsel in *P. frontalis* (see below). The fluorescent tubes in the three rooms all were on a 12L: 12D cycle, and the photophase started at 07:00 h. Lizards were housed individually in 200 × 200 × 200 mm glass cages. We fasted lizards at the test temperature for 3 d prior to feeding, and then fed them mealworms and provided water *ad libitum*. Trials lasted for 30–40 days to accumulate sufficient feces and urates for calorimetry. Feces, urates, and 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 $AE = 100 \times (I - F - U) / I$, where I = total energy consumed, F = energy in feces

and U = energy in urates; the apparent digestive coefficient was calculated as $ADC = 100 \times (I-F) / I$ (Lin et al., 2008).

1.4 Data analysis

All statistical analyses were performed with Statistica 6.0 for PC (Tulsa, OK, USA). We tested data for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using the Bartlett’s test. Preliminary linear regression analyses revealed that all variables examined in the two *Phrynocephalus* lizards were independent of body size (both mass and SVL). Therefore, we used two-way ANOVA with sex and species as the factors to examine whether thermal preference and thermal tolerance differed between the sexes and between the two species, repeated measures ANOVA with species as the between-subject factor and temperature as the within-subject factor to examine whether food passage time differed between the two species and among temperature treatments, and Two-Way ANOVA with species and temperature as the factors to examine whether food intake, ADC and AE differed between the two species and among temperature treatments. We used one-way ANOVA to examine whether thermal preference and thermal tolerance differed between lizards that differ in distribution, habitat use, or time use (temporal activity pattern), and whether the digestive coefficient was affected by the type of food ingested. Tukey’s test was used to show how many differences there were and where differences were located. Throughout this paper, values are presented as

mean \pm standard error (SE), and the significance level is set at $\alpha = 0.05$.

2 Results

Mean values for Tsel and CTMax both were greater in *P. versicolor* than in *P. frontalis*, but do not between the sexes; mean values for CTMin and VBT did not differ between the two species, nor between the sexes (Table 1). None of these four measures was affected by the species \times sex interaction (Table 1).

Food passage time differed among the six temperature treatments ($F_{5, 80} = 797.92, P < 0.0001$), but not between the two species ($F_{1, 16} = 0.02, P = 0.893$); the species \times temperature interaction was not a significant source of variation in this trait ($F_{5, 80} = 2.14, P = 0.069$). Food passage time decreased at an ever-decreasing rate as body temperature increased within the range of 24–40 °C in both species (Fig. 1).

Daily food intake, ADC and AE were independent of initial body mass within each species \times temperature combination (linear regression analysis; $P > 0.245$ in all cases). The two species differed in daily food intake but not in ADC and AE, with the mean daily food intake being greater in *P. frontalis* than in *P. versicolor* (Table 2). Body temperature affected daily food intake, ADC and AE (Table 2). Lizards at 24 °C daily ingested more food than did those at the two higher temperatures (Table 2). ADC and AE both were greatest in the 25 °C treatment and smallest in the 33 °C treatment, with the 39 °C treatment in between (Table 2).

Table 1 Data, expressed as mean \pm SE and range, on selected body temperature, critical thermal minimum, critical thermal maximum and viable temperature range for *P. frontalis* (PF) and *P. versicolor* (PV). All units are in °C, and results of Two-Way ANOVA with species and sex as the factors are given in the table

	<i>P. frontalis</i>		<i>P. versicolor</i>		Statistical results		
	Females	Males	Females	Males	Species	Sex	Interaction
<i>N</i>	10	10	10	10			
Selected body temperature	33.9 \pm 0.4 31.8–35.8	33.8 \pm 0.4 32.0–35.6	35.2 \pm 0.7 31.5–38.1	35.5 \pm 0.8 31.7–39.7	$F_{1, 36} = 5.85,$ $P = 0.021;$ PF < PV	$F_{1, 36} = 0.04,$ $P = 0.839$	$F_{1, 36} = 0.06,$ $P = 0.800$
Critical thermal minimum	1.3 \pm 0.2 0.4–2.0	1.3 \pm 0.1 0.7–2.0	1.4 \pm 0.3 0.4–3.1	1.2 \pm 0.2 0.1–2.9	$F_{1, 36} = 0.003,$ $P = 0.952$	$F_{1, 36} = 0.44,$ $P = 0.510$	$F_{1, 36} = 0.23,$ $P = 0.631$
Critical thermal maximum	47.2 \pm 0.3 46.0–49.1	47.6 \pm 0.4 46.3–50.0	48.0 \pm 0.3 46.6–49.8	48.2 \pm 0.3 46.3–50.5	$F_{1, 36} = 0.41,$ $P = 0.042;$ PF < PV	$F_{1, 36} = 0.84,$ $P = 0.366$	$F_{1, 36} = 0.01,$ $P = 0.906$
Viable temperature range	45.9 \pm 0.2 44.9–47.2	46.3 \pm 0.4 44.6–49.2	46.5 \pm 0.4 44.3–48.4	47.0 \pm 0.5 43.4–49.3	$F_{1, 36} = 2.84,$ $P = 0.101$	$F_{1, 36} = 1.25,$ $P = 0.271$	$F_{1, 36} = 0.03,$ $P = 0.864$

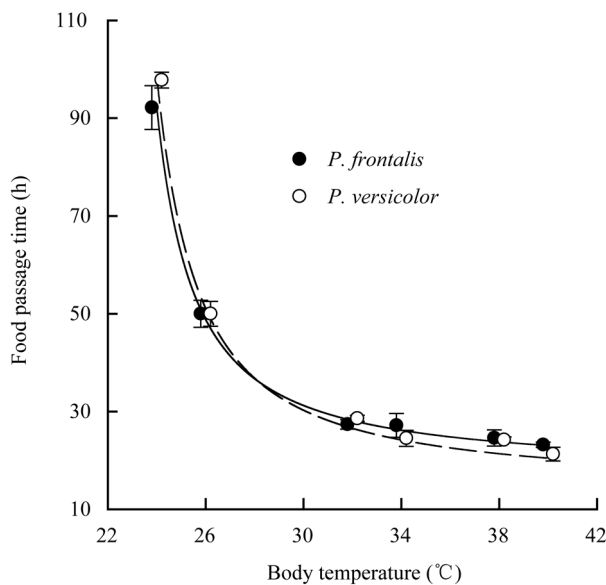


Fig. 1 Means (\pm SE) for food passage time of adult males at different body temperatures

The curves are generated from a negative exponential fit on the original data. The solid curve: *P. frontalis*; the dash curve: *P. versicolor*

3 Discussion

3.1 Thermal preference and thermal tolerance

Thermal environments in Inner Mongolia are characterized by the low mean temperatures and wide amplitude of thermal fluctuations. In such environments, the extent to which lizards are able to maximize their fitness is highly dependent on how well they can tolerate extreme temperatures. Not surprisingly, CTMin did not differ between the two coexisting lizards, as the lowest temperature they encounter in nature occurs during the periods of time not allowing behavioral thermoregulation and, spatially, varies little, if any, in the sympatric area covered by sparse vegetation. Adult *P. versicolor* selected higher body temperatures than adult *P. frontalis*, adding evidence that the set-point of thermoregulation may differ between congeneric lizards in the sympatric area (Ji et al., 1995; Du et al., 2000). Adult *P. versicolor* displayed a greater resistance to high temperatures than adult *P. frontalis* (This study), and the ability of embryos to tolerate high temperatures has been reported to be greater in *P. frontalis* than *P. versicolor* (Qu et al., 2011b). These observations provide an inference that habitats used by *P. versicolor* differ from those used by *P. frontalis* in thermal conditions. Niche divergence in the spatial dimension resulting from using thermally different habitats could be of importance in facilitating species coexistence by reducing interspecific competition for similar resources.

More than 90 species of lizards have been measured

for Tsel, with nearly a half of them measured for CTMin and CTMax (Appendix 1). Lizards from different climatic regions overall differ in Tsel ($F_{2,91} = 3.99$, $P = 0.022$), CTMin ($F_{2,41} = 5.54$, $P < 0.008$), CTMax ($F_{2,42} = 12.19$, $P < 0.0001$) and VBT ($F_{2,45} = 17.33$, $P < 0.0001$). Preferred body temperatures are generally highest in cold-climate lizards (34.0 °C) and lowest in warm-climate lizards (30.8 °C) (Tukey's test, $P < 0.05$), with temperate lizards (32.5 °C) in between (Fig. 2A). Overall, warm-climate lizards do not differ from temperate lizards in CTMin (Fig. 2B), CTMax (Fig. 2C) and VBT (Fig. 2D) (Tukey's test, $P > 0.979$ in all cases), whereas cold-climate lizards are better able to tolerate low and high temperatures and can therefore withstand a wider range of body temperatures than lizards from warmer climates (Tukey's test, $P < 0.003$ in all cases). CTMin is independent of Tsel ($F_{1,42} = 0.89$, $P = 0.350$; Fig. 3A), whereas CTMax is positively correlated with Tsel ($F_{1,43} = 45.15$, $P < 0.0001$; Fig. 3B). These findings are consistent with an earlier study focusing on Australian scincid lizards (Bennett and John-Alder, 1986).

We find in lizards from warm and temperate regions that: (1) diurnal species generally select higher body temperatures than nocturnal species (mean values = 32.5 °C versus 29.1 °C; $F_{1,85} = 14.64$, $P < 0.0003$), but they do not differ from nocturnal species in CTMin ($F_{1,37} = 0.03$, $P = 0.875$), CTMax ($F_{1,38} = 0.19$, $P = 0.662$) and VBT ($F_{1,37} = 0.19$, $P = 0.669$); and (2) lizards using open habitats with direct sun exposure generally select higher body temperatures (means = 32.5 °C versus 27.3 °C; $F_{1,85} = 26.67$, $P < 0.0001$) and are better able to tolerate high body temperatures (means = 42.3 °C versus 39.9 °C; $F_{1,38} = 7.89$, $P < 0.008$) than lizards using shaded habitats, but they do differ from lizards using shaded habitats in the ability to tolerate low body temperatures ($F_{1,37} = 3.10$, $P = 0.087$).

Excluding nocturnal lizards and diurnal lizards using shaded habitats (Appendix 1) from analyses, we find that lizards from different climatic regions differ in CTMin ($F_{2,35} = 4.85$, $P < 0.014$), CTMax ($F_{2,36} = 12.07$, $P < 0.0001$) and VBT ($F_{2,35} = 19.26$, $P < 0.0001$), but not in Tsel ($F_{2,70} = 1.60$, $P = 0.208$). Once again, warm-climate lizards do not differ from temperate lizards in CTMin, CTMax and VBT (Tukey's test, $P > 0.651$ in all cases), and cold-climate lizards are better able to tolerate low and high temperatures and can therefore withstand a wider range of body temperatures (Tukey's test on VBT, $P < 0.0002$ in both cases) than lizards inhabiting warmer regions (Tukey's test on CTMin and CTMax, $P < 0.02$ in all cases).

Table 2 Data, expressed as mean \pm SE and range, on initial body mass, daily food intake, apparent digestive coefficient (ADC) and assimilation efficiency (AE) for *P. frontalis* and *P. versicolor*. Results of two – way ANOVA with species and temperature as the factors are given in the table. Temperature treatments with different superscripts differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$; a > b)

	<i>P. frontalis</i>			<i>P. versicolor</i>			Statistical analysis		
	25 °C	33 °C	39 °C	25 °C	33 °C	39 °C	Species	Temperature	Interaction
<i>N</i>	17	20	21	17	20	22			
Initial body mass (g)	4.5 \pm 0.1 3.9–5.3	5.2 \pm 0.2 3.6–6.7	5.0 \pm 0.1 4.0–6.1	5.4 \pm 0.1 4.5–6.6	6.1 \pm 0.1 5.2–7.1	5.6 \pm 0.1 4.6–6.5	$F_{1,111} = 55.26$, $P < 0.0001$; PF < PV	$F_{2,111} = 13.14$, $P < 0.0001$; 25 ^b , 33 ^a , 39 ^a	$F_{2,111} = 0.91$, $P = 0.405$
Daily food intake (J·g ⁻¹ d ⁻¹)	372.5 \pm 44.0 100.0–756.8	346.2 \pm 24.3 126.4–521.7	283.3 \pm 21.0 84.9–468.2	343.3 \pm 28.4 138.9–623.7	174.9 \pm 13.5 65.5–247.4	218.2 \pm 22.9 79.4–564.5	$F_{1,111} = 17.20$, $P = 0.0002$; PF > PV	$F_{2,111} = 9.65$, $P < 0.0002$; 25 ^a , 33 ^b , 39 ^b	$F_{2,111} = 3.94$, $P = 0.022$
ADC (%)	95.0 \pm 0.4 90.0–96.7	90.3 \pm 0.4 85.5–92.8	93.5 \pm 0.7 86.3–97.9	94.9 \pm 0.5 87.8–97.2	90.1 \pm 0.8 81.2–94.6	93.3 \pm 0.7 86.7–97.7	$F_{1,111} = 0.10$, $P = 0.752$	$F_{2,111} = 27.77$, $P < 0.0001$; 25 ^a , 33 ^c , 39 ^b	$F_{2,111} = 0.003$, $P = 0.997$
AE (%)	90.8 \pm 0.8 80.5–93.2	82.4 \pm 0.5 78.6–86.5	88.0 \pm 1.2 74.9–95.8	90.8 \pm 0.6 83.4–93.5	81.2 \pm 1.2 64.0–88.3	85.1 \pm 1.7 73.9–95.5	$F_{1,111} = 2.30$, $P = 0.132$	$F_{2,111} = 29.90$, $P < 0.0001$; 25 ^a , 33 ^c , 39 ^b	$F_{2,111} = 0.80$, $P = 0.452$

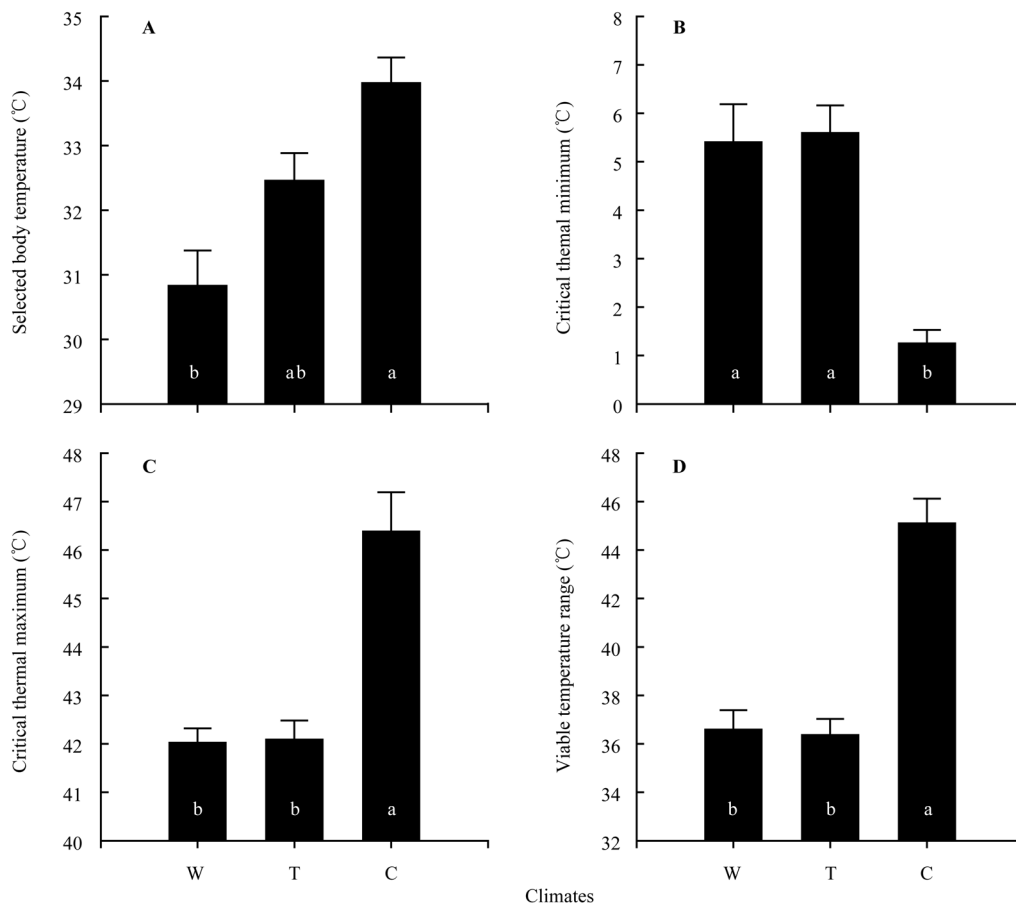


Fig. 2 Means (+SE) for selected body temperature (A), critical thermal minimum (B), critical thermal maximum (C), and viable temperature range (D) of lizards from different climatic regions

W, T and C represent warm-, temperate- and cold-climate lizards, respectively. Bars with different letters differ significantly (Tukey's test, $\alpha = 0.05$; $a > b$)

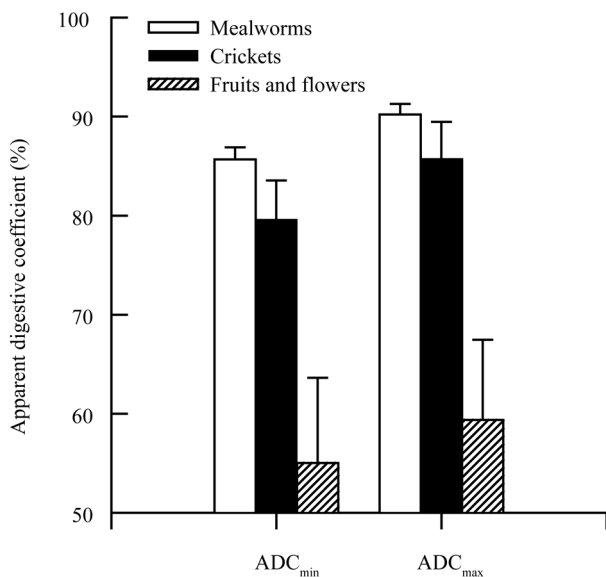


Fig. 3 Means (+SE) for the minimal (ADC_{min}) and maximal (ADC_{max}) values of ADC ever recorded in lizards fed with different types of food

3.2 Food passage time, food intake and food assimilation

Food passage time did not differ between *P. frontalis* and *P. versicolor* at any test temperature, and the species \times temperature interaction was not a significant source of variation in this measure of digestive performance. These findings suggest that the two lizards share the same pattern of temperature effects on food passage time, which is similar to that reported for *Uta stansburiana* (side-blotched lizard; Waldschmidt et al., 1986), *Takydromus septentrionalis* (northern grass lizard; Ji et al., 1996), *Eremias argus* (Mongolian racerunner; Luo et al., 2006) and *Calotes versicolor* (oriental garden lizard; Qiu et al., 2009) where food passage time decreases with increase in body temperature at an ever-decreasing rate (Fig. 1). There are another two patterns of temperature effects on food passage time in lizards. One is shared by *Eumeces chinensis* (Chinese skink; Ji et al., 1995), *Sphenomorphus indicus* (brown

forest skink; Ji et al., 1997), *Takydromus wolteri* (white-striped grass lizard; Chen et al., 2003) and *Hemidactylus bowringii* (oriental leaf-toed gecko; Xu et al., 2009) where food passage time decreases with increase in body temperature at lower temperatures and levels off at higher temperatures. The other is shared by *Lacerta (Zootoca) vivipara* (common lizard; Van Damme et al., 1991), *Sceloporus merriami* (Canyon lizard; Beaupre et al., 1993), *Eumeces elegans* (blue-tailed skink; Du et al., 2000), *Eremias brenchleyi* (Ordos racerunner lizard; Xu et al., 2001; Xu and Ji, 2006) and *Takydromus sexlineatus* (southern grass lizard; Zhang and Ji, 2004) where food passage time decreases with increase in body temperature at lower temperatures and then increases at higher temperatures. Interestingly, pattern differences occur at temperatures close to CTMax not maintained by lizards for prolonged periods of time in nature, and even congeneric lizards (e.g., *Eremias*, *Eumeces* and *Takydromus* lizards) may display different patterns over the range of body temperatures where feeding can occur (Xu and Ji, 2006).

The two *Phrynocephalus* lizards differed in daily food intake but not in ADC and AE (Table 2), two measures of digestive performance tightly correlated (Xu and Ji, 2006). The lack of the effects of the species \times temperature interaction on ADC and AE suggests that thermal sensitivities of these two measures of digestive performance do not differ between the two species. Individuals daily ingested more food at the lowest test temperature (25 °C) than at the two higher temperatures (33 °C and 39 °C) in both species. This result is somewhat unexpected, but is similar to those reported for *T. septentrionalis* (Ji et al., 1996) and *E. elegans* (Du et al., 2000). In many other lizards, individuals generally ingest more food at high temperatures than at low temperatures, largely due to the increased energy demands at high temperatures (Shu et al., 2010b and references therein). As in *Phrynocephalus vlangalii* (Qinghai toad-headed lizard; Shu et al., 2010b), ADC and AE were minimized at the intermediate body temperature in both *P. frontalis* and *P. versicolor*. In other lizard taxa including *Calotes*, *Eremias*, *Eumeces*, *Gekko*, *Hemidactylus* and *Takydromus* species, however, ADC and/or AE either are less thermally insensitive (Ji and Wang, 1990; Chen et al., 2003; Qiu et al., 2009), or reduce at body temperatures close to the lower and/or upper thermal thresholds at which feeding cannot occur (Ji et al., 1995; Du et al., 2000; Zhang and Ji, 2004; Luo et al., 2006; Xu and Ji, 2006; Xu et al., 2007; Li et al., 2009b).

Overall, ADC and AE are less thermally sensitive

than other measures of digestive performance such as food intake and food passage time. Until now, more than 40 lizard species have been measured for ADC, with less than one third of them measured for AE (Appendix 2). The minimal (ADCmin, $F_{2, 38} = 19.13$, $P < 0.0001$) and maximal (ADCmax, $F_{2, 38} = 22.24$, $P < 0.0001$) values of ADC are affected by the type of food ingested. Lizards ingesting mealworms overall do not differ from those ingesting crickets in ADCmin and ADCmax (Tukey's test, $P > 0.310$ in both cases), whereas lizards ingesting fruits and flowers displayed lower ADCmin and ADCmax than those ingesting mealworms and crickets (Tukey's test, $P < 0.0004$ in all cases) (Fig. 4). The mean values of ADC at the three test temperatures were inside the range (72.8%–96.0%) of

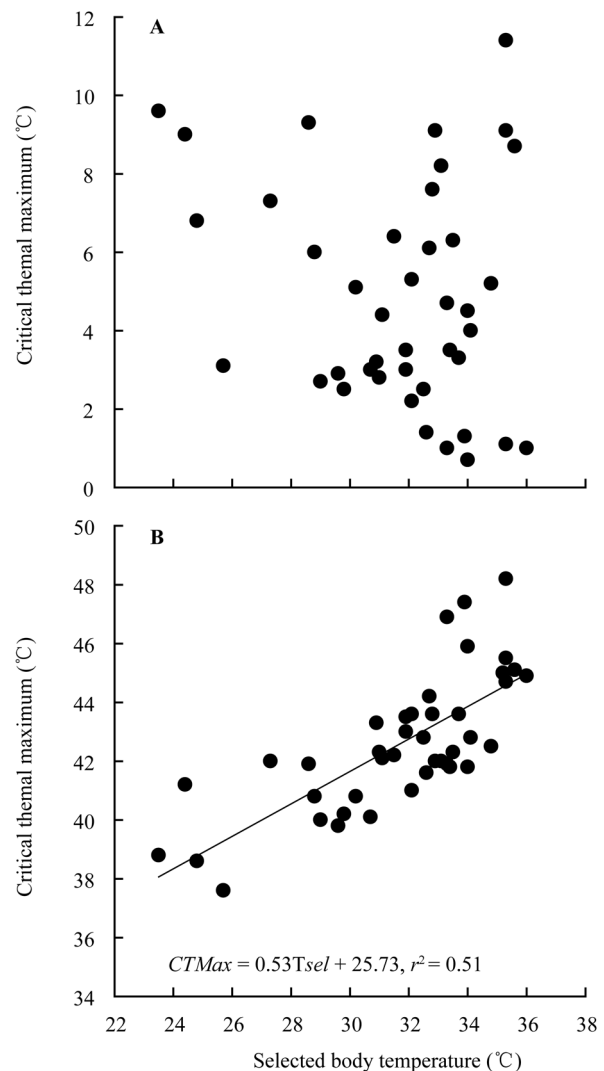


Fig. 4 The relationships between the lower (A, CTMin) and upper (B, CTMax) limits of thermal tolerance and thermal preference (Tsel) in lizards

Each dot represents one species.

ADCs reported for lizards ingesting mealworms (Table 2, Appendix 2) in both *P. frontalis* (90.3%–95.0%) and *P. versicolor* (90.1%–94.9%).

3 Conclusions

Available data allow us to draw the following four conclusions. Firstly, thermal preference and thermal tolerance differ among lizards that differ in distribution, temporal activity pattern and habitat use. Lizards living in thermally more variable regions are better able to tolerate low and high temperatures and can hence tolerate a wider range of body temperatures. Diurnal lizards generally select higher body temperatures than nocturnal lizards, and diurnal lizards using open habitats with direct sun exposure generally selected higher body temperatures and are better able to tolerate high temperatures than those using shaded habitats. Diurnal lizards overall do not differ from nocturnal lizards in the same climatic regions in thermal tolerance. Secondly, CTMax is positively correlated with Tsel. Lizards more likely exposed to extremely high temperatures while active select higher body temperatures than those using shaded habitats. The differences in Tsel and CTMax between *P. frontalis* and *P. versicolor* provide an inference that the two lizards use thermally different habitats in their sympatric area, and niche divergence in the spatial dimension resulting from differences in habitat use could be of importance in facilitating their coexistence. Thirdly, the effects of body temperature on measures (food intake, food passage time, ADC and AE) of digestive performance differ among lizards, but it seems to be common among lizards that ADC and AE are less thermally sensitive than food intake and food passage time. Lastly, ADC (and thus, AE) is highly dependent on the type of food ingested. The finding that ADCs are generally greater in lizards ingesting mealworms and crickets than in lizards ingesting fruits and flowers provides an inference that insectivorous lizards digest food more efficiently than herbivorous lizards.

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Appendix 1 Mean values for selected body temperature (Tsel), critical thermal minimum (CTMin) and critical thermal maximum (CTMax) of the lizards so far studied

Family Species	Tsel	CTMin	CTMax	References
Agamidae				
<i>Calotes versicolor</i> ¹	33.1	8.2	42.0	Qiu et al., 2009
<i>Chlamydosaurus kingii</i> ¹	33.7	–	–	Christian and Bedford, 1995
<i>Phrynocephalus frontalis</i> ³	33.9	1.3	47.4	This study
<i>Phrynocephalus versicolor</i> ³	35.3	1.1	48.2	This study
<i>Phrynocephalus vlangalii</i> ³	33.3	1.0	46.9	Shu et al., 2010b
Anguinae				
<i>Gerrhonotus multicarinatus</i> ²	33.6	–	–	Bennett, 1980
Chamaeleonidae				
<i>Chamaeleo bitaeniatus</i> ¹	31.1	4.4	42.1	Bennett, 2004
<i>Chamaeleo dilepis</i> ¹	32.8	7.6	43.6	Bennett, 2004
<i>Chamaeleo ellioti</i> ¹	33.4	3.5	41.8	Bennett, 2004
<i>Chamaeleo hohnelii</i> ¹	30.2	5.1	40.8	Bennett, 2004
<i>Chamaeleo jacksonii</i> ¹	32.1	5.3	41.0	Bennett, 2004
<i>Chamaeleo schubotzi</i> ¹	32.6	1.4	41.6	Bennett, 2004
Cordylidae				
<i>Platysaurus intermedius</i> ^{2,S}	31.2	–	–	Lailvaux et al., 2003
Crotaphytidae				
<i>Gambelia wislizenii</i> ²	35.4	–	–	Crowley and Pietruszka, 1983
Gekkonidae				
<i>Coleonyx brevis</i> ^{2,N}	31.8	–	–	Dial, 1978
<i>Coleonyx variegatus</i> ^{2,N}	28.6	–	–	Brattstrom, 1965
<i>Gekko japonicus</i> ^{2,N}	28.2	–	–	Hu and Du, 2007
<i>Hemidactylus bowringii</i> ^{1,N}	30.9	3.2	43.3	Xu et al., 2007, 2009
<i>Hemidactylus frenatus</i> ^{1,N}	31.8	–	–	Huey et al., 1989
<i>Hemidactylus turcicus</i> ^{2,N}	29.1	–	–	Angilletta et al., 1999
<i>Lepidodactylus lugubris</i> ^{1,N}	29.2	–	–	Heuy et al., 1989
<i>Sphaerodactylus gaigeae</i> ^{1,N}	27.6	–	–	Alvarez, 1992
<i>Sphaerodactylus klauberi</i> ^{1,N}	25.1	–	–	Alvarez, 1992
<i>Sphaerodactylus macrolepis</i> ^{1,N}	27.6	–	–	Alvarez, 1992
<i>Sphaerodactylus nicholsi</i> ^{1,N}	30.2	–	–	Alvarez, 1992
<i>Sphaerodactylus roosevelti</i> ^{1,N}	30.2	–	–	Alvarez, 1992
<i>Sphaerodactylus townsendi</i> ^{1,N}	30.2	–	–	Alvarez, 1992
Iguanidae				
<i>Dipsosaurus dorsalis</i> ²	38.5	–	–	Dewitt, 1967
Lacertidae				

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<i>Acanthodactylus erythrurus</i> ¹	37.2	–	–	Bauwens et al., 1995
<i>Eremias argus</i> ²	36.0	1.0	44.9	Luo et al., 2006
<i>Eremias brenchleyi</i> ²	33.7	3.3	43.6	Xu et al., 2001
<i>Eremias multiocellata</i> ³	34.0	0.7	45.9	Li et al., 2009b
<i>Eremias przewalskii</i> ³	34.5	–	–	Li et al., 2009a
<i>Gallotia simonyi</i> ²	36.8	–	–	Márquez et al., 1997
<i>Gallotia stehlini</i> ²	30.0	–	–	Márquez et al., 1997
<i>Lacerta agilis</i> ³	34.7	–	–	Bauwens et al., 1995
<i>Lacerta graeca</i> ²	33.2	–	–	Pafilis et al., 2007
<i>Lacerta monticola</i> ²	33.7	–	–	Bauwens et al., 1995
<i>Lacerta schreiberi</i> ²	35.3	–	–	Bauwens et al., 1995
<i>Podarcis atrata</i> ²	34.5	–	–	Bauwens et al., 1995
<i>Podarcis bocagei</i> ²	35.2	–	–	Bauwens et al., 1995
<i>Podarcis erhardii</i> ²	34.0	–	–	Pafilis et al., 2007
<i>Podarcis gaigeae</i> ²	33.8	–	–	Pafilis et al., 2007
<i>Podarcis hispanica</i> ²	34.4	–	–	Bauwens et al., 1995
<i>Podarcis lilfordi</i> ²	35.0	–	–	Bauwens et al., 1995
<i>Podarcis muralis</i> ²	34.0	–	–	Bauwens et al., 1995; Pafilis et al., 2007
<i>Podarcis peloponnesiaca</i> ²	33.9	–	–	Pafilis et al., 2007
<i>Podarcis tiliguerta</i> ²	35.5	–	–	Van Damme et al., 1989
<i>Psammodromus algirus</i> ²	35.4	–	–	Bauwens et al., 1995
<i>Psammodromus hispanicus</i> ²	35.1	–	–	Bauwens et al., 1995
<i>Takydromus septentrionalis</i> ²	30.0	3.9	42.3	Ji et al., 1996
<i>Takydromus sexlineatus</i> ¹	31.5	6.4	42.2	Zhang and Ji, 2004
<i>Zootoca vivipara</i> ³	32.1	2.2	43.6	Gvoždík and Castilla, 2001; Van Damme et al., 1986, 1991
Liolaemidae				
<i>Liolaemus elongatus</i> ¹	29.9	–	–	Ibarguengoytia, 2005
<i>Phymaturus patagonicus</i> ¹	31.1	–	–	Ibarguengoytia, 2005
Phrynosomatidae				
<i>Sceloporus graciosus</i> ²	32.8	9.1	43.6	Licht, 1965; Mueller, 1969
<i>Sceloporus occidentalis</i> ²	34.6	–	–	Bennett, 1980
<i>Sceloporus undulatus</i> ²	34.1	11.4	40.4	Crowley, 1987; Angilletta, 2001, Angilletta et al., 2002a
<i>Uma inornata</i> ²	37.0	–	–	Brattstrom, 1965
<i>Uta stansburiana</i> ²	35.5	–	–	Sartorius et al., 2002
Polychrotidae				
<i>Anolis carolinensis</i> ²	33.8	–	–	Martin and Huey, 2008
<i>Anolis cooki</i> ¹	30.6	–	–	Huey and Webster, 1976

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<i>Anolis cristatellus</i> ¹	29.4	–	–	Huey and Webster, 1976
<i>Anolis gundlachi</i> ^{1,S}	25.1	–	–	Huey and Webster, 1976
<i>Anolis lionotus</i> ^{1,S}	27.0	–	–	Campbell, 1971
Scincidae				
<i>Ctenotus regius</i> ²	35.6	8.7	45.1	Bennet and John-Alder, 1986
<i>Ctenotus taeniolatus</i> ²	35.3	11.4	44.7	Bennet and John-Alder, 1986
<i>Ctenotus uber</i> ²	35.3	9.1	45.5	Bennet and John-Alder, 1986
<i>Egernia cunninghami</i> ²	33.3	4.7	41.9	Bennet and John-Alder, 1986
<i>Egernia saxalilis</i> ²	34.0	4.5	41.8	Bennet and John-Alder, 1986
<i>Egernia striolata</i> ²	32.7	6.1	44.2	Bennet and John-Alder, 1986
<i>Egernia whitii</i> ²	34.1	4.0	42.8	Bennet and John-Alder, 1986
<i>Eremiascincus fasciolatus</i> ^{2,S}	24.4	9.0	41.2	Bennet and John-Alder, 1986
<i>Eremiascincus richardsoni</i> ^{2,N}	27.3	7.3	42.0	Bennet and John-Alder, 1986
<i>Eumeces chinensis</i> ²	33.5	6.3	42.3	Ji et al., 1995
<i>Eumeces elegans</i> ²	28.6	9.3	41.9	Du et al., 2000
<i>Hemiergis decresiensis</i> ^{2,S}	24.8	6.8	38.6	Bennet and John-Alder, 1986
<i>Hemiergis peroni</i> ^{2,S}	23.5	9.6	38.8	Bennet and John-Alder, 1986
<i>Leiopisma enlrecaleauxii</i> ²	32.5	2.5	42.8	Bennet and John-Alder, 1986
<i>Leiopisma melallicum</i> ²	29.0	2.7	40.0	Bennet and John-Alder, 1986
<i>Leiopisma ocellalum</i> ²	30.7	3.0	40.1	Bennet and John-Alder, 1986
<i>Leiopisma trilinealum</i> ²	31.9	3.0	43.5	Bennet and John-Alder, 1986
<i>Mabuya multifasciata</i> ¹	32.5	9.1	42.0	Ji et al., 2007; Sun, 2009*
<i>Pseudemoia spenceri</i> ²	31.0	2.8	42.3	Bennet and John-Alder, 1986
<i>Sphenomorphus indicus</i> ^{2,S}	25.7	3.1	37.6	Ji et al., 1997
<i>Sphenomorphus kosciuscoi</i> ²	29.8	2.5	40.2	Bennet and John-Alder, 1986
Family Species	Tsel	CTMin	CTMax	References
<i>Sphenomorphus quoyi</i> ²	28.8	6.0	40.8	Bennet and John-Alder, 1986
<i>Sphenomorphus tympanum</i> ²	29.6	2.9	39.8	Bennet and John-Alder, 1986
<i>Tiliqua nigrolutea</i> ²	34.8	5.2	42.5	Bennet and John-Alder, 1986
<i>Tiliqua rugosa</i> ²	31.9	3.5	43.0	Bennet and John-Alder, 1986
Teiidae				
<i>Cnemidophorus murinus</i> ¹	35.9	–	–	Vitt et al., 2005
<i>Cnemidophorus sexlineatus</i> ²	35.2	–	45.0	Witz, 2001
Xantusiidae				
<i>Xantusia riversiana</i> ^{2,N}	28.3	–	–	Mautz et al., 1992
<i>Xantusia vigilis</i> ^{2,N}	31.6	–	–	Kaufmann and Bennett, 1989

All units are in °C. Species with superscripts of 1, 2 and 3 are found in warm, temperate and cold climatic regions, respectively. Species with a superscript of N are nocturnally-active, and species with a superscript of S use shaded habitats covered by shrubs and/or trees.

* Sun YY, 2009. Life-history traits, thermal dependence of offspring phenotype and costs of tail loss in the many-lined sun skink *Mabuya multifasciata*. Master thesis, Hangzhou Normal University, Hangzhou, China.

Appendix 2 Mean values or the range of mean values for apparent digestive coefficients (ADC) and assimilation efficiencies (AE) of lizards under different thermal regimes

Species	Prey items	Temperature treatments (°C)	ADC (%)	AE (%)	References
Agamidae					
<i>Calotes versicolor</i>	Mealworms	26–34	80.7–83.6	70.9–75.2	Qiu et al., 2009
<i>Phrynocephalus frontalis</i>	Mealworms	24–40	90.6–95.0	82.5–90.7	This study
<i>Phrynocephalus versicolor</i>	Mealworms	24–40	90.6–94.9	81.9–90.8	This study
<i>Phrynocephalus vlangalii</i>	Mealworms	27–35	89.8–92.8	80.3–83.0	Shu et al., 2010b
Anguidae					
<i>Gerrhonotus multicarinatus</i>	Mealworms	20–30	89.0–91.2	–	Harwood, 1979
Cordylidae					
<i>Conolophus subcristatus</i>	Fruits	Natural temperatures	47.9	–	Christian et al., 1984
<i>Cordylus melanotus melanotus</i>	Mealworms	22–32	93.0–96.0	84.0–88.5	McConnachie and Alexander, 2004
<i>Platysaurus intermediu</i>	High quality diet	26–31	87.4–88.1	–	McKinnon and Alexander, 1999
<i>Platysaurus intermediu</i>	Lower quality diet	26–31	48.0–50.7	–	McKinnon and Alexander, 1999
Crotaphytidae					
<i>Crotaphytus collaris</i>	Flowers	20–37	25.7–32.4	–	Ruppert, 1980
<i>Crotaphytus collaris</i>	Crickets	20–37	56.3–65.5	–	Ruppert, 1980
Gekkonidae					
<i>Gekko japonicus</i>	Mealworms	18–33	–	76.1–84.6	Ji and Wang, 1990; Hu and Du, 2007
<i>Hemidactylus bowringii</i>	Mealworms	25–37	89.0–92.6	80.9–87.2	Xu et al., 2007, 2009
<i>Hemidactylus turcicus</i>	Crickets	27	87.0	72.4	Slade et al., 1994
Iguanidae					
<i>Ctenosaura pectinata</i>	Potato	24–43	86.4	–	Throckmorton, 1973
<i>Dipsosaurus dorsalis</i>	Rabbit food	33–41	54.3–69.5	–	Harlow et al., 1976
<i>Sauromalus obesus</i>	Flowers	20–37	65.1–66.6	–	Ruppert, 1980
<i>Sauromalus obesus</i>	Crickets	37	56.9–61.4	–	Ruppert, 1980
Lacertidae					
<i>Eremias argus</i>	Mealworms	28–38	91.8–95.7	81.8–88.2	Luo et al., 2006
<i>Eremias brenchleyi</i>	Mealworms	26–38	90.0–94.9	85.2–92.8	Xu et al., 2001
<i>Eremias multiocellata</i>	Mealworms	28–38	88.6–93.2	80.2–88.3	Li et al., 2009
<i>Lacerta graeca</i>	Mealworms	20–30	72.8–75.1	–	Pafilis et al., 2007
<i>Podarcis erhardii</i>	Mealworms	20–30	80.2–85.1	–	Pafilis et al., 2007

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<i>Podarcis gaigeae</i>	Mealworms	20–30	79.3–83.7	–	Pafilis et al., 2007
<i>Podarcis muralis</i>	Mealworms	20–30	73.0–85.1	–	Pafilis et al., 2007
<i>Podarcis peloponnesiaca</i>	Mealworms	20–30	74.5–84.4	–	Pafilis et al., 2007
<i>Takydromus septentrionalis</i>	Mealworms	26–36	91.4–93.6	86.2–89.1	Ji et al., 1996
<i>Takydromus sexlineatus</i>	Mealworms	24–36	84.2–90.0	77.2–84.1	Zhang and Ji, 2004
<i>Takydromus wolteri</i>	Mealworms	26–34	90.5–93.3	84.4–88.8	Chen et al., 2003
<i>Zootoca vivipara</i>	Crickets	20–35	86.0–92.0	–	Van Damme et al., 1991
Phrynosomatidae					
<i>Sceloporus merriami</i>	Crickets	31–36	85.9–94.3	77.0–79.5	Beaupre et al., 1993
<i>Sceloporus occidentalis</i>	Mealworms	26–36	84.2–88.9	–	Harwood, 1979
<i>Sceloporus olivaceus</i>	Crickets	15–30	81.0–89.0	–	Dutton et al., 1975
<i>Sceloporus undulatus</i>	Crickets	30–36	87.0–92.0	75.0–82.0	Angilletta, 2001, Angilletta et al., 2002a
<i>Sceloporus undulatus</i>	Crickets	20–36	82.0–88.0	71.0–77.0	Angilletta, 2001
<i>Uta stansburiana</i>	Crickets	22–36	84.0–93.0	–	Waldschmidt et al., 1986
Polychrotidae					
<i>Anolis carolinensis</i>	Mealworms	Natural temperatures	79.7–82.0	–	Kitchell and Windell, 1972
<i>Anolis limifrons</i>	Crickets	20–28	88.4	–	Andrews and Asato, 1977
Scincidae					
<i>Eumeces chinensis</i>	Mealworms	24–36	83.4–93.9	73.3–88.5	Ji et al., 1995
<i>Eumeces elegans</i>	Mealworms	22–36	89.5–92.4	81.7–87.0	Du et al., 2000
<i>Mabuya multifasciata</i>	Mealworms	26–30	90.1–91.8	83.8–85.1	Lin et al., 2008
<i>Sphenomorphus indicus</i>	Mealworms	26–32	90.2–91.7	81.9–85.1	Ji et al., 1997
Teiidae					
<i>Cnemidophorus tigris</i>	Mealworms	27–35	85.7–94.5	–	Harwood, 1979
Varanidae					
<i>Varanus niloticus</i>	Mouse	22–35	89.7–93.6	–	Buffenstein and Louw, 1982
Xantusiidae					
<i>Klauberina riversiana</i>	Mealworms	20–31	93.0	85.3	Johnson and Lillywhite, 1979
<i>Klauberina riversiana</i>	Apple	20–31	89.1	87.8	Johnson and Lillywhite, 1979