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Northern grass lizards (*Takydromus septentrionalis*) from different populations do not differ in thermal preference and thermal tolerance when acclimated under identical thermal conditions

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Abstract We acclimated adults of *Takydromus septentrionalis* (northern grass lizard) from four localities (populations) under identical thermal conditions to examine whether local thermal conditions have a fixed influence on thermal preference and thermal tolerance in the species. Selected body temperature (Tsel), critical thermal minimum (CTMin), and critical thermal maximum (CTMax) did not differ between sexes and among localities in lizards kept under identical laboratory conditions for ~5 months, and the interaction effects between sex and locality on these measures were not significant. Lizards acclimated to the three constant temperatures (20, 25, and 35°C) differed in Tsel, CTMin, and CTMax. Tsel, CTMin, and CTMax all shifted upward as acclimation temperature increased, with Tsel shifting from 32.0 to 34.1°C, CTMin from 4.9 to 8.0°C, and CTMax from 42.0 to 44.5°C at the change-over of acclimation temperature from 20 to 35°C. Lizards acclimated to the three constant temperatures also differed in the range of viable body temperatures; the range was widest in the 25°C treatment (38.1°C) and narrowest in the 35°C treatment (36.5°C), with the 20°C treatment in between (37.2°C). The results of this study show that local thermal conditions do not have a fixed influence on thermal preference and thermal tolerance in *T. septentrionalis*.

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Introduction

Temperature is the single most important environmental factor affecting many biological processes in organisms (Cossins and Bowler 1987). In ectotherms, for example, environmental temperature influences body temperature, which in turn, affects not only physiological processes but also behavioral performances that are linked to these processes (Huey and Stevenson 1979; Bennett 1980; Huey 1982; Huey and Kingsolver 1989; Angilletta et al. 2002). Prolonged exposure of animals to extremely low or high temperatures may lead to death (Hutchison 1979). The upper and lower critical thermal limits [critical thermal maximum (CTMax) and critical thermal minimum (CTMin), respectively] have been defined as the temperatures at the upper and lower extremes of tolerance at which the animal cannot right itself when placed on its back, i.e., the loss of righting response (Lowe and Vance 1955; Hutchison 1961; Doughty 1994; Lutterschmidt and Hutchison 1997). Whereas ectotherms are viable under a wide range of body temperatures, their physiological processes, and behavioral performances are usually maximized at moderate to relatively high body temperatures. It is therefore not surprising that many ectotherms attempt to maintain relatively high and constant body temperatures when conditions allow for it (Huey 1982; Huey and Kingsolver 1989, 1993; Navas et al. 1999; Angilletta et al. 2002). Ectotherms heavily rely on behavioral mechanisms such as habitat selection, basking intensity, restriction of activity periods and selective exploitation of environmental thermal flux to acquire and maintain appropriate body temperatures (Cowles and Bogert 1944; Avery 1982; Bartholomew 1982; Huey 1982, 1991). Body temperatures preferred or selected by ectotherms broadly fall within the range of temperatures allowing them to express their physiological or behavioral performances at relatively high levels (Hutchison 1976; Hertz et al. 1993; Christian and Weavers 1996; Blouin-Demers et al. 2000; Angilletta et al. 2002).

Selected body temperature (Tsel) and thermal tolerance (CTMax and CTMin) have been examined in a wide variety of taxa, and lizards are among the most extensively studied taxa. Previous studies generally show that Tsel, CTMax, and CTMin vary among lizard species as a response to changes in thermal environments associated with habitat use or geographic variation in climate (Huey and Kingsolver 1993; Feder et al. 2000; Angilletta et al. 2002; Winne and Keck 2005). For example, lizards such as *Sphenomorphus indicus* (brown forest skink) using shaded or cold habitats select relatively low body temperatures (~26°C; Ji et al. 1997), whereas those such as *Eumeces chinensis* (Chinese skink) using open or warm habitats select relatively high body temperatures (~31°C; Ji et al. 1995). A recent laboratory study of thermal preference and thermal tolerance in warm versus cold populations of *Takydromus septentrionalis* (northern grass lizard) show that individuals (adult males) from the cold population select lower body temperatures (31.5°C vs. 32.7°C) but do not differ significantly from those from the warm population in CTMin (3.4°C vs. 3.6°C) and CTMax (41.2°C vs. 41.5°C) (Du 2006). These values are somewhat inconsistent with those reported for another population of *T. septentrionalis* in Zhoushan Islands, where Tsel, CTMin, and CTMax of adult males are 30.0, 3.9, and 42.3°C, respectively (Ji et al. 1996). Among population differences in Tsel, CTMin, and CTMax seen in *T. septentrionalis* raise a question of whether local thermal conditions have a fixed influence on thermal preference and thermal tolerance in lizards. Where such variation solely results from the effects of environmental or thermal acclimation, we hypothesize that individuals from different localities (populations) do not differ in Tsel, CTMax, and CTMin when they are acclimated under identical thermal conditions.

Here, we describe a study acclimating adults of *T. septentrionalis* from different localities under identical thermal conditions (see below for details) to test our hypothesis. This oviparous lacertid lizard is endemic to China and lives mainly in the southern provinces of the country (Ji et al. 2007). Adults are sexually dimorphic in head size but not in body size, and large females lay up to seven clutches per breeding season stretching from April to August (Zhang and Ji 2000; Du et al. 2005; Ji et al. 2007). The lizard can be easily maintained in the laboratory and is able to maintain a relatively high and constant body temperature when thermal conditions allow for it (Du et al. 2000; Shou et al. 2005), and therefore offers an excellent model system to test our hypothesis.

Materials and methods

Animal collection and maintenance

Adults of *T. septentrionalis* [60–80 mm snout-vent length (SVL)] were captured in early April 2006 from four localities (populations). One locality is in Shengsi (30°43′N, 122°27′E), Zhoushan Islands; the other three are situated on the mainland: Lishui (28°46′N, 119°92′E), Ningbo (29°56′N, 121°51′E), and Qinling (34°09′N, 108°55′E). Data on monthly mean air temperature show differences in thermal environment among the four localities (Fig. 1). Lizards were transported to our laboratory in Hangzhou, where they were marked via unique combinations of clipped toes. Nine to 12 individuals randomly selected from different populations were housed together in each (length × width × height: 90 × 65 × 50 cm^3) glass terrarium with moist soil, pieces of clay tile, and grasses. Terrariums were placed in a room kept at 23–28°C. A 100 W light bulb, suspended at one end of each cage, created a thermal gradient from the room temperature 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 (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals ad libitum. Females completed their oviposition cycles in the laboratory.

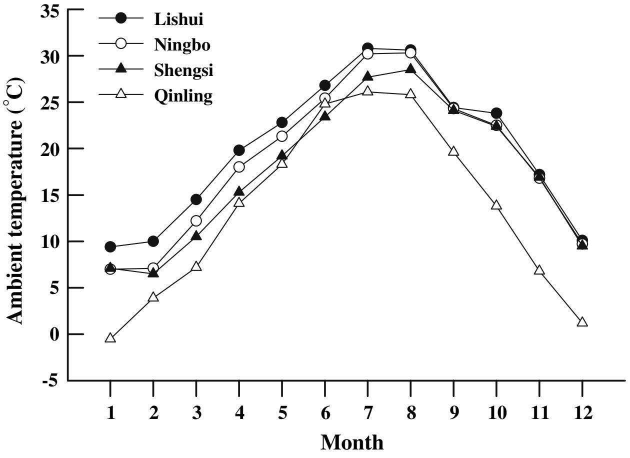

Fig. 1 Monthly mean air temperatures for 1986–2006 at the four localities (courtesy of the Provincial Bureaus of Meteorology of Zhejiang and Shaanxi), where lizards were collected. The annual mean temperatures in Lishui (*filled circle*), Ningbo (*open circle*), Shengsi (*filled triangle*), and Qinling (*open square*) are ~20.0, 18.7, 17.6, and 13.4°C, respectively. Activities are rare for *T. septentrionalis* at air temperatures lower than 14°C (the *horizontal line*) (Ji et al. 1994)

Experimental design

A total of 404 lizards (Lishui: 19♀♀/21♂♂, 60–73 mm SVL; Ningbo: 47♀♀/65♂♂, 61–76 mm SVL; Shengsi: 86♀♀/109♂♂, 62–75 mm SVL; Qinling: 35♀♀/22♂♂, 62–80 mm SVL) were measured for Tsel, CTMin, or CTMax in September, when lizards from different populations had been kept under identical thermal conditions for ~5 months. Lizards from each of the four localities were divided into three groups that were measured for Tsel, CTMin, and CTMax, respectively. This experiment allows examination of the extent to which thermal preference and thermal tolerance vary as a fixed response to local thermal environments.

In October, a total of 240 lizards (120♀♀/120♂♂) were randomly sampled from the above individuals to examine the effects of thermal acclimation on Tsel, CTMin, and CTMax. These lizards were equally divided into three groups of which each was assigned to one of the three temperature treatments (20°C: 40♀♀/40♂♂; 25°C: 40♀♀/40♂♂; 35°C: 40♀♀/40♂♂). Lizards were acclimated in their designated temperature treatments for 3 weeks, followed by Tsel, CTMin, or CTMax measurements. During this time the lizards did not have a heat source for basking and, according to the results reported previously for the species (Wang and Xu 1987), the body temperatures of the test groups should be constant and very close to 20, 25, or 35°C. In each treatment, 40 (20♀♀/20♂♂), 20 (10♀♀/10♂♂), and 20 (10♀♀/10♂♂) individuals were measured for Tsel, CTMin, and CTMax, respectively. This experiment allows examination of the extent to which thermal preference and thermal tolerance vary not as a fixed response to changes in thermal environment.

Measurements of Tsel, CTMin, and CTMax

We measured Tsel in 100 × 80 × 50 cm^3 glass terrariums with 5 cm depth moist soil and pieces of clay tiles. Two 100 W light bulbs suspended above one end of the terrarium created a thermal gradient from the room temperature (20°C) to 50°C for 12 h daily. Eight to ten lizards were synchronously introduced into the gradient at the cold end at 0600 (Beijing time) when the lights were switched on. We began measurements every trial day at 1,500 and ended within 2 h, thereby minimizing the possible influence of diel variation in Tsel (Hutchison 1976; Firth and Belan 1998; Angilletta et al. 1999). Body (cloacal) temperatures (to the nearest 0.1°C) were taken for lizards that were basking on the surface of the substrate using a UT325 digital thermometer (Shanghai Medical Instruments, China), which had been calibrated using a standard thermometer (Yunrun Instruments, China). The probe (1 mm diameter) of the digital thermometer was inserted ~5 mm into the cloacae when used to measure a lizard's body temperature, and great care was taken to avoid heat transfer occurring between the hand and the lizard. To address the repeatability of our measurements, we measured each lizard twice, once on each of two consecutive days. The two measures did not differ significantly (paired-sample *t*-test; $P > 0.10$ in all cases), so we considered the mean of the two measures as an individual's Tsel.

Critical thermal minimum and CTMax were determined using FPQ incubators (Ningbo Life Instruments, China). Trials were conducted during 1,000–1,500. We cooled (for CTMin determination) or heated (for CTMax determination) lizards from their designated acclimation temperatures 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 trials, we observed the behavior of lizards through a window in the incubator door. Lizards were taken out of the incubator for the righting response test, and 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 thermal tolerance were considered to be the endpoints for CTMin and CTMax, respectively (Ji et al. 1995).

Data analysis

We used Statistica software package (Version 5.0 for PC) to analyze data. All data were tested for normality using Kolmogorov-Smirnov test, and for homogeneity of variances using Bartlett's test. No data required transformation to satisfy the assumptions for parametric tests, and body size (SVL) was not a significant source of variation in Tsel, CTMin, and CTMax in each case. We used two-way ANOVA to test the effects of sex and locality on Tsel, CTMin, and CTMax, and one-way ANOVA to test the effects of acclimation temperature on these measures. Descriptive statistics are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$.

Results

Two-way ANOVAs with sex and locality as the factors revealed that Tsel, CTMin, and CTMax did not differ between sexes and among localities in lizards kept under identical laboratory conditions for ~5 months, and that the interaction effects between sex and locality on these measures were not significant (Table 1). Two-way ANOVAs on data from the second experiment (with lizards acclimated to the three constant temperatures) revealed that sex, locality, and their interaction did not have significant effects in each of the three temperature treatments (all $P > 0.331$). Sex and

Table 1 Descriptive statistics for Tsel, CTMin, and CTMax (in °C) of northern grass lizards collected from four localities that had been acclimated under identical laboratory conditions for ~5 months

Locality		Selected body temperature		Critical thermal minimum		Critical thermal maximum	
		Female	Male	Female	Male	Female	Male
Lishui		32.6 ± 0.4 (8)	33.8 ± 0.3 (9)	5.2 ± 0.1 (4)	5.4 ± 0.1 (7)	43.2 ± 0.1 (7)	43.0 ± 0.5 (5)
		31.6–34.4	32.4–35.4	4.9–5.5	5.0–5.9	42.8–43.5	41.4–44.0
Ningbo		33.2 ± 0.4 (20)	33.2 ± 0.2 (24)	5.3 ± 0.06 (15)	5.2 ± 0.1 (21)	43.5 ± 0.1 (12)	43.2 ± 0.1 (20)
		29.9–36.2	31.5–35.7	5.0–5.6	4.2–5.9	42.9–44.1	42.0–43.9
Shengsi		32.6 ± 0.2 (32)	33.1 ± 0.2 (44)	5.3 ± 0.06 (28)	5.3 ± 0.07 (40)	43.5 ± 0.1 (26)	43.3 ± 0.2 (25)
		29.6–34.6	30.9–35.5	4.7–5.8	4.0–5.9	41.5–44.2	40.3–44.1
Qinling		33.6 ± 0.4 (11)	33.0 ± 0.4 (7)	5.4 ± 0.07 (12)	5.7 ± 0.1 (8)	43.2 ± 0.2 (12)	43.2 ± 0.3 (7)
		31.8–36.0	31.5–34.5	5.0–5.7	5.0–5.9	41.3–43.6	41.8–44.0
Effects	Locality	$F_{3,147} = 1.05, P = 0.308$		$F_{3,127} = 2.35, P = 0.075$		$F_{3,106} = 0.46, P = 0.708$	
	Sex	$F_{1,147} = 1.31, P = 0.273$		$F_{1,127} = 1.85, P = 0.176$		$F_{1,106} = 1.70, P = 0.195$	
	Interaction	$F_{3,147} = 2.08, P = 0.106$		$F_{3,127} = 1.41, P = 0.242$		$F_{3,106} = 0.27, P = 0.850$	

Data are expressed as mean ± SE and range. Numbers in parentheses are sample sizes

locality were therefore ignored for subsequent analyses. One-way ANOVAs revealed that lizards kept at different temperatures for 3 weeks differed in Tsel ($F_{2,117} = 49.85$, $P < 0.0001$), CTMin ($F_{2,57} = 280.96$, $P < 0.0001$), and CTMax ($F_{2,57} = 58.99$, $P < 0.0001$). Tsel, CTMin, and CTMax all shifted upward as acclimation temperature increased, with Tsel shifting from 32.0 to 34.1°C, CTMin from 4.9 to 8.0°C, and CTMax from 42.0 to 44.5°C at the change-over of acclimation temperature from 20 to 35°C (Fig. 2). Lizards acclimated to the three different constant temperatures differed in the range of viable body temperatures (i.e., the difference between CTMax and CTMin) ($F_{2,57} = 71.60$, $P < 0.0001$); the range was widest in the 25°C treatment (38.1°C) and narrowest in the 35°C treatment (36.5°C), with the 20°C treatment in between (37.2°C) (Fig. 2).

Discussion

Thermal preference and thermal tolerance are affected by both extrinsic and intrinsic factors, including acclimation regime, photoperiod, geography, sex, age, and physiological state (Patterson and Davies 1978; Lutterschmidt and Hutchison 1997; Andrews 1998; Rock et al. 2000; Brown and Griffin 2005). Thus, in order to make data collected from different species or different localities (populations) comparable and biologically meaningful, it is important to use controlled or standardized methods or experimental procedures such as acclimating animals to known temperatures prior to measurements. Unfortunately, many studies in this field neglect to indicate acclimation temperature or period. The major drawback associated with this negligence is that data may be of little value in comparison of inherent thermal preference and thermal tolerance because differences within and among species can reflect seasonal or geographical differences in environmental conditions (Soulé 1963; Graham and Hutchison 1979). In earlier studies of *T. septentrionalis* (Ji et al. 1996; Shou et al. 2005; Du 2006), for example, Tsel, CTMin, and CTMax were measured for lizards that were not acclimated at any known temperatures prior to measurements and, as such, it is hard to distinguish between extents to which thermal preference and thermal tolerance vary as and not as a fixed response to local thermal conditions.

Consistent with studies of other ectotherms (e.g., Hutchison 1961; Brattstrom 1968, 1971; Jacobson and Whitford 1970; Patterson 1999; Huang et al. 2006; Gvoždík et al. 2007), the results of this study show that thermal acclimation significantly affects Tsel, CTMin, and CTMax in *T. septentrionalis* (Fig. 2). There are two interesting findings in this study. One is that lizards from different localities did not exhibit any differences in thermal preference and thermal tolerance when they were acclimated under identical thermal conditions (Table 1). This finding suggests that geographic variation in thermal preference and thermal tolerance seen in *T. septentrionalis* (Du 2006) is unlikely determined evolutionarily as a consequence of adaptation to local thermal conditions. The other is that the range of viable body temperatures was wider in lizards acclimated to 25°C than in those acclimated to 20 or 35°C (Fig. 2). This finding suggests that maintaining low or high body temperatures, often during the cold (winter) or hot (summer) months or time phases when activities are rare (Ji et al. 1994), may lead to decreased abilities to tolerate extreme temperatures in *T. septentrionalis*. It worth noting, however, that a more limited thermal tolerance does not matter if extreme temperatures never occur. For example, lizards

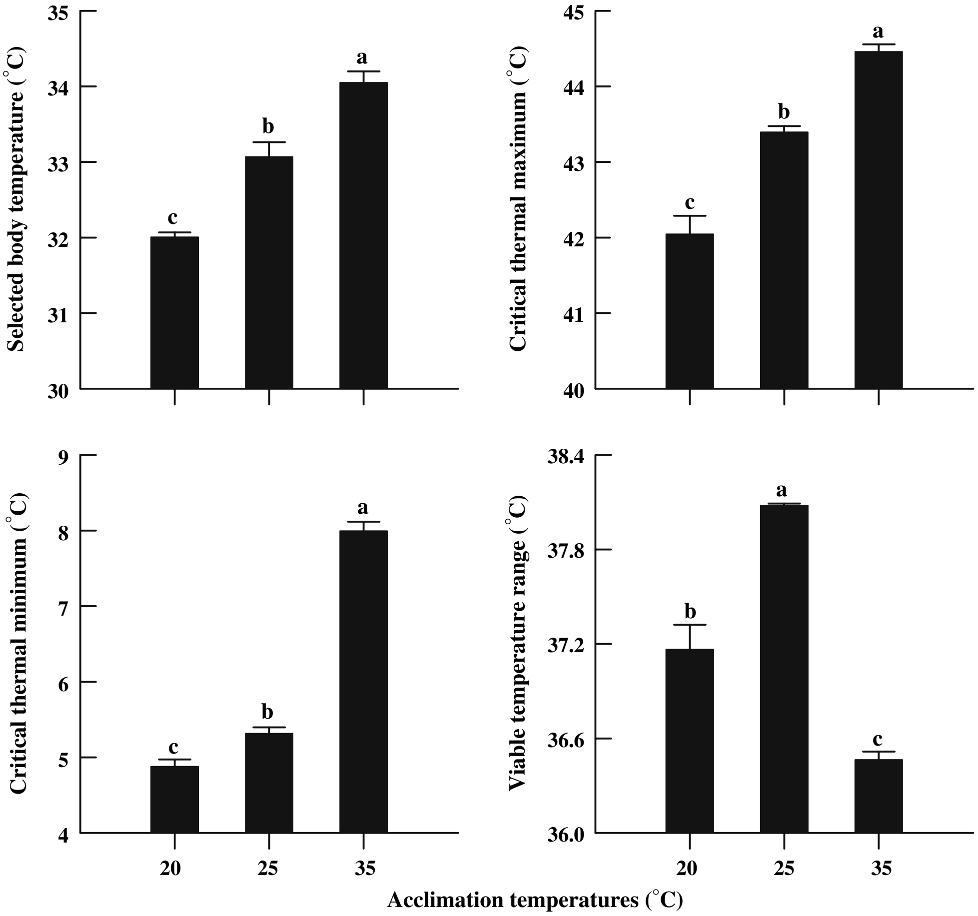

Fig. 2 Mean values (+SE) for selected body temperature, critical thermal minimum, critical thermal maximum, and viable temperature range of lizards acclimated at different temperatures. Means with different superscripts differ significantly (Tukey's post hoc test, $\alpha = 0.05$; $a > b > c$)

acclimated to summer temperatures are very unlikely to experience extremely low-ambient temperatures, and lizards acclimated to winter temperatures are very unlikely to encounter extremely high-ambient temperatures.

Du (2006) found that lizards from the cold population selected lower body temperatures but did not differ from those from the warm population in CTMin and CTMax. Given that Tsel, CTMin, and CTMax all shift upward as acclimation temperature increases, and vice versa (Fig. 2), why did lizards from the two populations differ in Tsel but not in CTMin and CTMax in Du's (2006) study? The answer presumably lies in the effects of thermal acclimation. Du (2006) commenced Tsel measurements soon after lizards were collected from the field, and CTMin and CTMax measurements ~3 weeks later. During the trial intervals, he maintained lizards from the two populations under identical laboratory conditions. Therefore, according to the experimental sequence in his study, lizards measured for Tsel were actually acclimated to natural thermal conditions, whereas lizards measured for CTMin and CTMax were acclimated to laboratory thermal conditions. Du (2006) did not find any differences in CTMin and CTMax between the cold and warm populations, primarily because maintaining *T. septentrionalis* from different localities under identical laboratory conditions for 3 weeks is long enough to remove the influence of natural thermal conditions on thermal tolerance. Therefore, results reported by Du (2006) do not actually contradict to those of this study but provide indirect evidence that thermal acclimation plays an important role in determining thermal preference and thermal tolerance in *T. septentrionalis*.

As in *Sceloporus* and *Liolaemus* lizards (Jaksic and Schwenk 1983; Marquet et al. 1989; Andrew 1998), field body temperatures vary geographically in *T. septentrionalis* (Ji et al. 1996; Shou et al. 2005). The body temperature at which ectotherms in nature try to maintain can be estimated by measuring Tsel (Hutchison 1976). Nonetheless, field body temperature is rarely consistent with Tsel because thermoregulation in nature can be affected by numerous biotic and abiotic factors (Hutchison 1976; Andrews 1998; Shou et al. 2005). Thermoregulation may result in potential fitness benefits, but the benefits are offset by any costs associated with thermoregulation in a given environment (Shine and Madsen 1996; Sartorius et al. 2002). The results of this study show that northern grass lizards are capable of shifting Tsel according to changes in thermal environment. Given that Tsel represents the body temperature yielding relatively high physiological or behavioral performances (e.g., Van Damme et al. 1991; Hertz et al. 1993; Christian and Weavers 1996; Blouin-Demers et al. 2000; Angilletta et al. 2002), do shifts in Tsel entail costs associated with reduced performances in *T. septentrionalis*? Our answer to this question is negative: for example, body temperatures varying over a relatively wide range (28–36°C) do not have differential effects on several important performances such as food intake, food assimilation and locomotion in the species (Ji et al. 1996). Northern grass lizards have the potential to maintain relatively high and constant body temperatures in a variety of thermal environments by modifying thermoregulatory activities (Ji et al. 1996; Shou et al. 2005), but such modification often entails costs associated with increased energetic demands and predation risks (Ji et al. 1994). Thus, shifting thermal preference according to changes in thermal environment is likely a mechanism evolved in *T. septentrionalis* to reduce costs associated with thermoregulation in thermally variable environments.

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