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Locomotor and Elevational Distribution of a Mountainous Lizard, *Takydromus hsuehshanensis*, in Taiwan

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Shu-Ping Huang and Ming-Chung Tu (2009) Locomotor performance and elevational distribution of a mountainous lizard, *Takydromus hsuehshanensis*, in Taiwan. *Zoological Studies* **48**(4): 477-484. We investigated the impact of environmental temperature on elevational distributions of a high-mountainous lizard, *Takydromus hsuehshanensis*, by examining the thermal sensitivity of its locomotor performance. Its sprint speed was measured at 9 body temperatures after 2 wk of acclimation at 2 different temperatures. The same measurements were performed on a closely related species, *T. formosanus*, which lives at lower elevations. The results indicated that (1) *T. hsuehshanensis* was capable of maintaining normal locomotor performance within a body temperature range which approximates summer temperatures of lowland areas; (2) *T. formosanus* was able to run significantly faster than *T. hsuehshanensis* within a certain range of body temperatures; (3) these 2 species did not differ in their thermal sensitivities of the locomotor performance; and (4) temperature acclimation treatments did not affect the locomotor performance of these 2 species. We concluded that locomotor performance is not a crucial factor limiting the distribution of *T. hsuehshanensis* in lowland areas. http://zoolstud.sinica.edu.tw/Journals/48.4/477.pdf

Key words: Lizards, Temperature, Locomotion, Distribution, Elevation.

A species' geographic range is affected by environmental factors (such as temperature, humidity, and oxygen content) and biotic factors (i.e., predators, competition, parasitism, etc.) (Krebs 1994). Among environmental factors, temperature is a particularly important factor affecting the geographic ranges of ectotherms (Graham et al. 1971, Greer 1980, Huang et al. 2006) because of its impact on their body temperature (Brattstrom 1965). Body temperature often greatly influences physiological functions and behavioral performance of ectotherms (Bennett 1980, Kaufmann and Bennett 1989).

Temperature changes dramatically with elevation (McCullough and Portor 1971). Although reptiles are capable of adjusting their body temperature behaviorally (Spellerberg 1972, Huey and Pianka 1977, Avery 1982, Hertz and Huey 1981, Huey 1982), they cannot fully compensate for thermal differences among different thermal environments due to associated costs (Huey 1974). Some mountainous reptiles thus have a field body temperature lower than that of their lowland counterparts (Hertz et al. 1983, van Berkum 1986, van Damme et al. 1989). To compensate for the effect of cold temperature on their performance, some montane ectotherms have physiological adjustments, such as being more tolerant to cold (Heatwole et al. 1969, Huang et al. 2006, Huang and Tu 2008a) or performing better at lower temperatures (Hillyard 1981, Beuchat et al. 1984, Navas 1996) compared to their lowland counterparts.

The ability of an animal to perform specific ecological activities well, such as escaping predators or capturing prey, affects its survival, reproduction, and growth (Arnold 1983, Pough 1989, Wainwright 1994). Locomotor performance is a whole-animal measure that is intimately linked to fitness. It affects an individual's fitness in critical

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activities such as capturing prey (Jayne and Bennett 1990, Husak et al. 2006) and escaping predators (Christian and Tracy 1981, Husak et al. 2006). Locomotor performance is therefore a relevant ecological measure of physiological performance in ectotherms.

Since locomotor performance of ectotherms is dramatically affected by temperature (Bennett 1980), we proposed that high-elevation ectotherms restricted to mountainous areas would have different temperature-dependent locomotor capacities to cope with cold temperatures. On the other hand, this different locomotor capacity may hinder these ectotherms from dispersing to lower elevations. In this study, we sought to determine whether the locomotor capacity of an endemic grasslizard, *Takydromus hsuehshanensis*, is related to its elevational distribution. *Takydromus hsuehshanensis* is only distributed at elevations above 1800 m in Taiwan (Lue et al. 1999). We earlier found that its heat tolerance is not a crucial factor affecting its current distribution (Huang and Tu 2008b). We measured the thermal sensitivity of its locomotor performance to see if that is an important factor affecting its elevational distribution. We used a closely related species, *T. formosanus* (recently revised as *T. viridipunctatus*, Lue and Lin, 2008), which lives at elevations lower than 1500 m as a reference (Lue et al. 1999). Several important descriptive statistics such as the “optimal” T_b (herein defined as the body temperature, T_b, at best performance; see Fig. 1) and the “thermal performance breadth” (B_{80} and B_{95}, herein defined as the range of T_b values in which an animal performs well; see Fig. 1) were used to examine their thermal sensitivities (Huey and Stevenson 1979, van Berkum 1986). In addition, to evaluate whether locomotor performance can be adjusted by short-term temperature exposure, we also examined their locomotor performance after 2 wk of acclimation at 2 different temperatures (10 and 30°C).

We proposed that locomotor performance of *T. hsuehshanensis* would be impeded at higher temperatures which approximate summer temperatures occurring in lowland areas. When compared at higher temperatures, *T. hsuehshanensis* was predicted to run more slowly than *T. formosanus*. As to thermal sensitivity, because *T. hsuehshanensis* lives in a habitat with a more-variable and lower mean temperature, we predicted that *T. hsuehshanensis* would have a lower T_{opt} or broader performance breadth relative to *T. formosanus*. In addition, we predicted that warm-acclimated individuals would run faster than cold-acclimated ones when compared at a high T_b, but would run more slowly than cold-acclimated individuals when compared at a low T_b.

MATERIALS AND METHODS

Animal collection

From May to Sept. 2005 and 2007, we collected *T. hsuehshanensis* (mean ± 1 SD) (weight = 4.75 ± 1.1 g; snout-vent length (SVL) = 62.6 ± 4.1 mm; *n* = 47) from Mt. Hehuan (2400-3200 m in

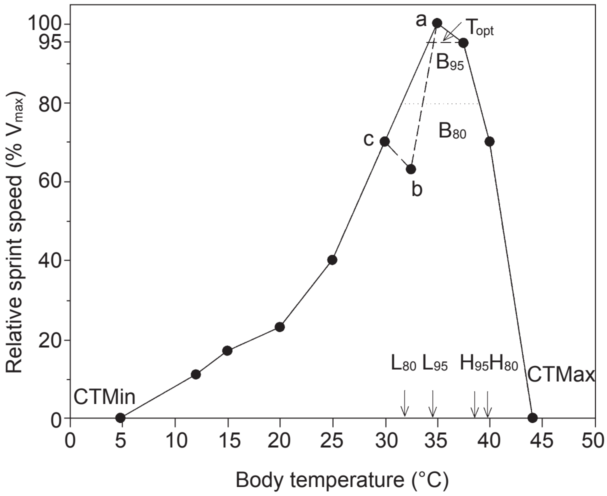

Fig. 1. Schematic diagram illustrating the analysis of sprint speed data and the variables used to describe the thermal sensitivity of the sprint speed. For each lizard, the fastest sprint speed measured at each body temperature (T_b) was transformed to a relative speed (see “Materials and methods”). Solid circles indicate the relative sprint speed of a *T. hsuehshanensis* (with a body weight of 4.45 g and a snout-vent length of 63.8 mm). The relative sprint speed was set to 0 at the mean CTMin and CTMax reported by Huang and Tu (2008a b). Point “a” indicates the fastest speed (V_{max}, 100%). Since point “b” is lower than its adjacent points, “a” and “c”, it was considered too low and was excluded (van Berkum 1985). As proposed by van Berkum (1986), we drew a line connecting points “a” and “c” for further analysis. L_{95} and L_{80} are the lowest T_b values at which a lizard is able to run 95% and 80% of its maximum sprint speed, respectively; H_{95} and H_{80} are the highest T_b values at which a lizard is able to run 95% and 80% of its maximum sprint speed, respectively; B_{95} and B_{80} are the T_b range at which a lizard is able to run at least 95% and 80% of its maximum sprint speed, respectively. The T_{opt} is the midpoint of L_{95} and H_{95}, which is defined as the T_b at which a lizard can run the fastest. The dotted lines are performance breadths (Huey and Stevenson 1979), defined as the range of T_b over which a lizard can run 95% (B_{95}) and 80% (B_{80}) of its fastest speed.

elevation, Nantou County, central Taiwan). At the same time, we collected *T. formosanus* (mean ± 1 SD) (weight = 2.5 ± 0.4 g, SVL = 50.8 ± 3.1 mm, *n* = 45) from Taipei County at elevations below 600 m. To prevent a potential effect of pregnancy, we only used male lizards in this study. We housed the animals individually in a plastic container (length × width × height = 20 × 10 × 15 cm) with a layer of soil and dry grass as the substrate; a piece of tile served as a shelter in a constant-temperature room (~25°C,12 h light (L):12 h dark (D)) before the animals were acclimated to the temperatures used in our study. Food (crickets and mealworms dusted with vitamin powder) was provided about every 3 d, and water was provided ad libitum. Body mass was monitored before and during the experiment as a health indicator. Lizards that lost over 20% of their original body mass were excluded (*n* = 3).

Acclimation temperature treatments

Individuals from each species were randomly assigned to 2 temperature groups (10 and 30°C). Each group of the same species contained lizards of approximately the same mean body mass. Before taking measurements, the lizards were put into a thermal incubator set to 10 or 30°C, with a photoperiod of 12 h L: 12 h D for 2 wk. They were provided with food (crickets and mealworms dusted with vitamin powder) every 3 d and water ad libitum. They were starved for 2 d before taking measurements to prevent an effect of digestion on locomotor performance.

Experimental protocol

We measured the sprint speeds of these lizards at 9 different temperatures ranging from 12 to 40°C. We assigned 40°C as the highest temperature because it was 3-4°C lower than their critical thermal maximum (Huang and Tu 2008b). The 9 temperature measurements were set in a fixed sequence as follows: 20, 25, 15, 30, 32, 12, 35, 37.5, 20, and 40°C. The order of the first 8 settings was randomly chosen, but the order of the last 2 settings was purposely set. We assigned the 40°C setting last because it might cause a harmful effect to the lizards; we used the 20°C setting a 2nd time to verify the health condition of the lizards. If a lizard could not maintain a maximum speed higher than 80% of the 1st 20°C setting, we would exclude the data collected from that individual; however, we did not need to exclude any data for this reason. Before taking measurements, we placed a test lizard in a temperature-controlled walk-in chamber set to the test temperature for at least 2 h. Each lizard then ran 2 trials at these temperature settings except at 40°C, at which only 1 trial was run. In the preliminary test, we observed that some lizards (5 of 20 tested lizards) showed abnormal behaviors, such as flaccid legs or lolling tongues after they were kept at 40°C for more than 4 h. Thus, we only conducted 1 trial at the 40°C setting. Each trial included 3 runs, and the tested individuals were given a break of about 4 h between trials. A 2 d interval was used between each set of temperature measurements. The animals were maintained at their original acclimation temperature settings between each experimental test.

The sprint speeds were measured using a treadmill (length × width × height = 150 × 20 × 25 cm). The treadmill had 16 pairs of infrared timing photocells installed on both side walls, with each photocell separated by a distance of 10 cm. We used a soft plastic stick to chase the lizards down the treadmill. The time it took the lizards to run each 10 cm distance was recorded. We calculated 20 cm sprint speeds by dividing 20 cm by the total time it took the lizard to run every 2 adjacent 10 cm distances. We then selected the fastest speed among the 6 runs at each temperature for further analysis. The frequency of the maximum speed that occurred in the 1st and 2nd runs did not significantly differ in these tested individuals (p = 0.65, by Chi-squared test).

Examination of the performance curve

We refer to the performance curve as the relationship between T_b and the relative sprint speed (van Berkum 1986, Huey and Kingsolver 1989). We transformed the absolute maximum sprint speed of each individual into its relative sprint speed (%) by dividing it by the fastest sprint speed of that individual measured over all experimental temperatures. We drew a plot of the relative sprint speeds versus temperature for each lizard by connecting the relative sprint speeds at the 9 test temperatures (as shown in Fig. 1). Following van Berkum (1985), if a value for a sprint speed was lower than its 2 adjacent sprint speeds (i.e., point “b” in Fig.1), this value in question was considered too low and was excluded. We then adjusted the questionable data point to an adjusted value by linearly interpolating it from its adjacent pairs of points (see Fig. 1). When a lizard had more than 1 sprint speed value in question, we excluded the data of that lizard (*n* = 4).

From the performance of each lizard, we extracted the lower and higher bounds of T_b at which a lizard can run at 80% of its fastest speed (i.e., L_{80} and H_{80}, respectively) and at which the lizard can run at 95% of its fastest speed (i.e., L_{95} and H_{95}, respectively) (see text of Fig. 1). The optimal T_b (i.e., T_{opt}), defined as the T_b at which a lizard can run its fastest speed, was calculated as the midpoint between L_{95} and H_{95}. The 80% and 95% performance breadths (i.e., B_{80} and B_{95}, respectively) were calculated by substracting H_{80} from L_{80} and H_{95} from L_{95}, respectively.

Data analysis

To test the effects of species, temperature, and their interactions on the thermal sensitivity, 7 measures (i.e., L_{80}, L_{95}, H_{80}, H_{95}, B_{80}, B_{95}, and T_{opt}) were subjected to a multivariate analysis of variance (MANOVA). We analyzed the effects of species, acclimation treatment, and their interaction on the absolute sprint speed, using a two-way repeated MANOVA with 9 absolute sprint speeds as the dependent variables. We chose the model using an autoregressive heterogeneous structure as the covariance structure after comparing the statistical fit values (AIC and -2LRR) with those of models using other covariate structures (unstructured, compound symmetrical, and autoregressive). SAS Proc MIXED was employed to perform the statistical analysis and the SLICE option in the LSMEAN statement was used to compare significant differences among groups when the significance level was reached ($\alpha = 0.05$). All statistical analyses were performed with SAS software (vers. 9.1.3, SAS institute).

RESULTS

We detected no significant effects of species (MANOVA, Wilks' $\Lambda_{5,84} = 0.98$, $p = 0.73$), acclimation temperature (MANOVA, Wilks' $\Lambda_{5,85} = 0.88$, $p = 0.06$), or their interaction (MANOVA, Wilks' $\Lambda_{4,85} = 0.73$, $p = 0.60$) on the thermal sensitivity of the locomotor performance (i.e., L_{80}, H_{80}, L_{95}, H_{95}, B_{80}, B_{95}, and T_{opt}). Table 1 shows the parameters of the locomotor performance of these 2 species. These 2 species had a mean L_{80} and mean H_{80} which fell in a range of 30.4-31.3 and 37.8-38.9°C, respectively. Their B_{80} ranged 6.4-8.2°C. Their mean L_{95} and mean H_{95} were in a range of 33.0-34.0 and 35.6-36.6°C, respectively. The B_{95} ranged 2.5-3.0°C , and their mean T_{opt} fell in the range of 34.3-35.3°C.

Figure 2 indicates the absolute sprint speeds of these 2 species measured at different T_b values. *Takydromus hsuehshanensis* ran significantly more slowly than did *T. formosanus* ($F_{1,88} = 21.6$, $p < 0.0001$), but there was no significant effect of acclimation temperature treatments ($F_{1,88} = 0.28$, $p = 0.59$) or the interaction ($F_{1,88} = 1.23$, $p = 0.26$) on the absolute sprint speed (two-way repeated MANOVA). A post hoc analysis revealed that *T. formosanus* exhibited a significantly higher sprint speed than did *T. hsuehshanensis* at T_b values above 20°C, but when measured at 12 or 15°C, their sprint speeds did not significantly differ from each other.

DISCUSSION

The results falsified our prediction that *T. hsuehshanensis* would have an impeded locomotor performance in a high temperature range which

Table 1. Thermal sensitivity of the sprint speed in *Takydromus hsuehshanensis* and *T. formosanus* at 2 acclimation temperatures. L_{95} and L_{80} are the lowest body temperature (T_b) at which lizards are able to run 95% and 80% of the maximum sprint speed, respectively; H_{95} and H_{80} are the highest T_b at which lizards are able to run 95% and 80% of the maximum sprint speed, respectively; B_{95} and B_{80} are the T_b width at which a lizard is able to run at least 95% and 80% of maximum sprint speed, respectively. Values are the mean ± 1 standard error

Species	Acclimation temperature	L_{95} (°C)	H_{95} (°C)	B_{95} (°C)	L_{80} (°C)	H_{80} (°C)	B_{80} (°C)	T_{opt} (°C)	*n*
T. hsuehshanensis	10°C	33.0 ± 0.5	36.4 ± 0.5	3.0 ± 0.3	30.7 ± 0.5	38.9 ± 0.4	8.2 ± 0.6	35.0 ± 0.4	20
	30°C	33.7 ± 0.4	36.3 ± 0.4	2.5 ± 0.3	31.3 ± 0.4	37.8 ± 0.3	6.4 ± 0.5	35.0 ± 0.4	27
T. formosanus	10°C	33.0 ± 0.5	35.6 ± 0.5	2.6 ± 0.3	30.4 ± 0.5	38.3 ± 0.4	7.8 ± 0.6	34.3 ± 0.4	21
	30°C	34.0 ± 0.4	36.6 ± 0.6	2.5 ± 0.3	31.5 ± 0.5	38.2 ± 0.3	8.2 ± 0.6	35.3 ± 0.4	24

approximated summer temperatures of lowland areas. Its mean T_{opt} fell in the range of 34.3-35.3°C, which is higher than regular summer temperatures of lowland areas. According to records from the Central Weather Bureau, Taiwan (1971-2000), the monthly mean maximum summer temperature measured in 3 lowland cities in northern (Taipei), west-central (Taichung), and southern (Kaohsiung) Taiwan fell in the range of 31.5-33.0°C. Clearly, lowland summer temperatures do not exceed the T_{opt} of *T. hsuehshanensis* and thus would not be too high to reduce *T. hsuehshanensis*' locomotor performance. Accordingly, *T. hsuehshanensis*' locomotor performance is not a crucial biotic constraint affecting its elevational distribution. Because *T. hsuehshanensis* ran more slowly than *T. formosanus*, *T. hsuehshanensis* would probably be at a disadvantage if it lived sympatrically with *T. formosanus*. Further experiments concerning interspecific competition would be helpful in clarifying our interpretation.

We also found that the thermal sensitivities of the locomotor performance these 2 *Takydromus* lizards did not significantly differ. Hertz et al. (1983) used "static" and "labile" to describe the thermal sensitivity of reptilian thermal physiology. In the "static" view, traceable to Bogert (1949), thermal physiology is evolutionarily conserved and resistant to directional selection (i.e., different thermal environments). Results of our study support the "static" view. Similar findings were reported for other species living at different elevational gradients (interspecific comparisons of *Agamid* lizards by Hertz et al. 1983, and intraspecific comparisons of *Sceloporus undulatus* by Crowley 1985 and of *Podarcis tiliguerta* by van Damme et al. 1989). On the other hand, the "labile" view argues that species or populations do respond to divergent thermal environments by making adaptations in their thermal physiology. Results of the locomotor performance coming from *Anolis* lizards living at different elevation gradients support the "labile" view (van Berkum 1986).

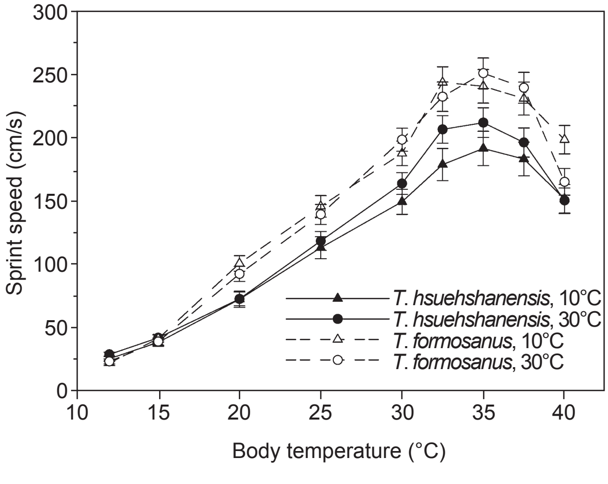

Fig. 2. Absolute sprint speeds (estimated mean ± 1 standard error) of *Takydromus hsuehshanensis* and *T. formosanus* at different body temperatures with 2 different acclimation temperatures (10 and 30°C). Sample size: *T. hsuehshanensis*, 10°C, *n* = 20; 30°C, *n* = 27; *T. formosanus*, 10°C, *n* = 21; 30°C, *n* = 24.

A possible explanation for differences in the above studies may be related to the effectiveness of thermal regulation behaviors in these ectotherms. Hertz (1981) proposed that "species which use thermal regulatory behaviors to compensate for altitudinal changes in thermal environment exhibit less geographical variation in their sensitivity to high temperature than do the thermoconformers". Huey et al. (2003) also postulated that thermoregulatory behaviors likely inhibit selection for evolutionary shifts in a lizard (*Anolis cristatellus*). This was true for similar heat thermal tolerances (the critical thermal maximum) of 3 *Takydromus* lizards that are distributed in different elevational ranges (Huang and Tu 2008b). We suspect that the similar sprint speeds of these 2 species can be explained by their effective thermoregulatory behaviors. In table 2, we collected data regarding locomotor performances of ectotherms that live at different elevational gradients. We examined whether the difference in thermal sensitivities of locomotor performance among closely related species or populations are related to thermoregulatory behaviors. We defined behavioral thermoregulators into 2 categories of "poor" or "good". Amphibians are generally considered to be poor thermoregulators due to conflicts of the requirements for respiration and hydroregulation with those for thermoregulation (Hutchison and Dupre 1992). Thus, we classified all amphibians as "poor" behavioral thermoregulators. In terms of reptiles, we defined species that do not have basking behavior as "poor" thermoregulators. We found that effective behavioral thermoregulators, such as some lizards (Crowley 1985, van Damme et al. 1989), followed the "static" view of ectotherm thermal physiology. In contrast, those ineffective behavioral thermoregulators, such as some frogs (Navas 1996) and some anoles (van Berkum 1986), followed the "labile view". Obviously, the thermal sensitivity of the locomotor performance is closely associated with the effectiveness of behavioral thermoregulation in these ectotherms.

We detected no significant temperature acclimation effects on the sprint speeds of these 2 *Takydromus* lizards, indicating that their locomotor performances were not affected by the previous short-term thermal history. These results are consistent with previous studies (on anoles by van Berkum 1985, on box turtles by Adams 1989, on salamanders by Else and Bennett 1987, and on anurans by Putnam and Bennett 1981, Renaud and Stevens 1983, Whitehead et al. 1989, Knowles and Weigl 1990, and Wilson and Franklin 2000). On the contrary, some ectotherms are able to improve locomotor performance based on the temperatures to which they are exposed (in fish by Beddow et al. 1995, Johnson and Bennett 1995, and Tample and Johnston 1998, in anurans by Wilson and Franklin 1999, in toads by Londos and Brooks 1988, and in salamanders by Feder 1986 and Marvin 2003).

In summary, we found that *T. hsuehshanensis* did not have impeded locomotor performance at high temperatures which are similar to summer temperatures in lowland areas. Thus, the sprint

Table 2. Thermal sensitivity of locomotor performance and behavioral thermoregulation in some amphibians and reptiles living at different elevations

Species	Elevation (m)	Thermal sensitivity parameters		Behavioral thermoregulation	Reference
		T_{opt} difference	B_{80} difference		
Interspecific comparison					
Amphibians					
Atelopus					
A. sp. nov.	3500	-	Yes	Poor	Navas 1996
A. varius	350			Poor	
Colostethus					
C. subpunctatus	3500	-	Yes	Poor	
C. flotator	90			Poor	
Eleutherodactylus					
E. bogotensis	3500	-	Yes	Poor	
E. diastema	90			Poor	
Hyla					
H. labialis	2900	-	Yes	Poor	
H. microcephala	90			Poor	
H. ebraccata	90			Poor	
Lizards					
Anolis[1]					
A. tropidolepis	1400-2600	Yes	Yes	Poor	van Berkum 1986
A. limifrons	lowlands			Poor	
A. humilis	0-1500			Poor	
A.lemurinus	lowlands			Poor	
A. intermedius	1200-1800			Good	
A. lionotus	0-1300			Good	
A. cupreus	low to mid elevations		Good		
Inter-population comparison					
Podarcis tiliguerta	0-70 and 1450	No	No	Good	van Damme et al. 1989
Sceloporus undulatus	1750 and 2350-2400	No[a]	No[a]	Good[b,c]	[a]Crowley 1985 [b]Kennedy 1958 [c]Behler 1979

[1] Differences of thermal sensitivities among these 7 *Anolis* species were compared together in the original paper. Therefore, we are not able to separately show differences in thermal sensitivities among "Good" thermoregulators and "Poor" thermoregulators.

speed of *T. hsuehshanensis* is likely not a crucial factor limiting its current elevational distribution. So far, we have demonstrated that neither heat tolerance nor locomotor performances of *T. hsuehshanensis* are critical factors limiting its current elevational distribution. Nevertheless, environmental temperature may still play an important role in its elevational distribution through other aspects of thermal physiology. For example, there is a profound thermal effect on embryo development (Packard et al. 1977, Packard and Packard 1988, Chen 2008) and hatchling phenotypes (Booth 2006), which may consequently play important roles in the geographic distributions of reptiles (Parker and Andrews 2007). Further investigations on juvenile survivorship and fecundity are needed to examine the role that temperature plays in the elevational distribution of *T. hsuehshanensis*. Other than temperature effects, biotic factors such as predators, competition, and parasitism, may all interact to affect the distribution of animals. By examining each factor step by step, we may eventually clarify the factors limiting its distribution.

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