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Cold Tolerance and Altitudinal Distribution of *Takydromus* Lizards in Taiwan

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Shu-Ping Huang and Ming-Chung Tu (2008) Cold tolerance and altitudinal distribution of *Takydromus* lizards in Taiwan. *Zoological Studies* **47**(4): 438-444. We investigated whether cold tolerance was an important limiting factor in the current altitudinal distributions of two *Takydromus* lizards, *T. formosanus* (< 1500 m in altitude) and the lowland-dwelling *T. stejnegeri* (< 1000 m in altitude) in Taiwan. We measured their critical thermal minimum (CTMin) and 3 mo survival rates in 4 cold treatments, and compared these with a high-mountainous species, *T. hsuehshanensis* (> 1800 m in altitude). The results indicated that (1) both the CTMin and prolonged cold tolerance were correlated to their upper limit of altitudinal distributions as predicted and (2) *T. formosanus* and *T. stejnegeri* had reasonable survival rates at temperatures that were lower than the underground temperature of high altitudinal areas. We concluded that although cold tolerance was correlated with altitudinal distribution, it is not a crucial factor limiting *T. formosanus* and *T. stejnegeri* at higher altitudes.
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Key words: Ectotherms, Temperature, CTMin, Mountain, Distribution.

The geographical distributions of ectotherms may be influenced by a variety of environmental factors, such as temperature, humidity, and oxygen content (Campbell and Solórzano 1992, Krebs 1994, Gaston 2003). Among these factors, temperature is particularly important (Stuart 1951, Graham et al. 1971, Huang et al. 2006) because the body temperature of ectotherms is largely dependent on heat exchange with the physical environment (Pough 1980). Although ectotherms are capable of behaviorally regulating their body temperatures (Brattstrom 1965 1970a 1979, Spellerberg 1972a, Huey and Pianka 1977, Hertz and Huey 1981, Huey 1982) to reduce the impacts of ambient temperatures, their physical environments eventually limit the extent of behavioural thermoregulation (Huey 1974, Huey and Stevenson 1979, Wu and Kam 2005). Since body temperatures dramatically affect a variety of physiological functions and behavioral performance (Bennett 1980, Kaufmann and Bennett 1989, Angilletta 2001), we expected that environmental temperatures might affect the survival of ectotherms and consequently their geographic distribution ranges.

As temperature decreases with altitude, high altitudinal ectotherms experience lower temperatures than their low altitudinal congeners (van Damme et al. 1989 1990, Grant and Dunham 1990, Smith and Ballinger 1994, reviewed by Navas 2003). Thus, a cold environment might foster cold tolerance for closely related species in higher altitudinal areas. Indeed, there is a positive correlation between altitudinal distribution and cold tolerance of some ectothermic vertebrates (lizards: Spellerberg 1972a 1973, Huang et al. 2006; amphibians: Brattstrom 1968). Also, some lowland ectotherms suffered death from direct exposure to cold temperatures that approximated high mountain temperatures (amphibians: Wei and Hou 2004; lizards: Heatwole et al. 1969, Gorman and Hillman 1977, Huang et al. 2006).

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We measured the cold tolerance of 3 *Takydromus* lizard species distributed at different altitudes in Taiwan. Traditionally, the critical thermal minimum (CTMin) is used as an important index of the cold tolerance of animals. It is the body temperature at which an animal's locomotion activity becomes disorganized, and the animal presumably cannot escape from conditions that will promptly lead to its death (Cowles and Bogert 1944, Lowe and Vance 1955, Hutchison 1961). Nevertheless, the CTMin can reveal only the short-term tolerance of an animal. We examined prolonged thermal tolerance as well because an animal might be able to tolerate cold temperatures for short periods of time but not for long periods of time (Gorman and Hillman 1977, Huey 1982, Huang et al. 2006). Therefore, in this study we measured both the CTMin and 3 mo survival rates to provide information on the cold tolerance over different time scales.

We attempted to determine whether cold tolerance was critical in limiting the distribution of two *Takydromus* species at different high altitudes. In Taiwan, *T*. *stejnegeri* and *T*. *formosanus* are only found below 1000 and 1500 m, respectively, whereas *T*. *hsuehshanensis* occurs only above 1800 m (Lue et al. 1999). We measured and compared the cold tolerances, both CTMin and prolonged cold tolerance (i.e., the survival rate) under cold treatments of these 3 species. Since an ectotherm's CTMin may change with acclimation temperatures (Brattstrom and Regal 1965, Brattstrom 1970b, Hutchison and Ferrance 1970), the CTMin was measured after a 2 wk acclimation at 3 temperatures. Their survival rates were accessed under 4 cold treatments over a 3 mo period. We also collected data on winter temperatures in a high altitudinal area to infer the impacts of field temperatures on their altitudinal distributions. We predicted that 1) these 3 *Takydromus* lizards' cold tolerances would correlate with the upper limit of their altitudinal distributions; and 2) *T. stejnegeri* and *T. formosanus* could not survive cold temperatures similar to those of the high altitudinal area, consequently limiting their current altitudinal distributions.

MATERIALS AND METHODS

Animal collection and maintenance

From May to Oct. 2004 and 2005, we collected *Takydromus hsuehshanensis* (female: mass = 4.1 ± 0.1 g, *n* = 33; male: mass = 4.4 ± 0.1 g, *n* = 74) (mean ± 1 standard error (S.E.)) from Nantou County. During the same time, we collected *T*. *stejnegeri* (female: mass = 2.9 ± 0.1 g, *n* = 32; male: mass = 2.6 ± 0.1 g, *n* = 87) from Taoyuan and Taipei Counties and *T*. *formosanus* (female: mass = 2.9 ± 0.1 g, *n* = 32; male: mass = 2.6 ± 0.1 g, *n* = 60) from Taipei County. The specimens of *T. formosanus* that we collected in this study were revised as *T. viridipunctatus* in recent publication (Lue and Lin 2008). We measured the CTMin values in the lizards' active seasons. All females were excluded to prevent a potential pregnancy effect on CTMin values. We tested the survival rate during the winter in both males and females.

Animals collected before Aug. were used for the CTMin measurement, and animals collected after Aug. were used for the prolonged survival test. In the laboratory, animals were individually housed in plastic boxes (length x width x height of 20 x 10 x 15 cm) containing a layer of soil and dry grass as substrates and a piece of tile as a shelter. Animals were kept in a temperature-controlled room (~25°C, with a 12: 12 h light (L): dark (D) photoperiod) before the experiments. They were provided with food (crickets and mealworms dusted with vitamin powder) every 3-4 d and water *ad libitum*.

Critical thermal minimum (CTMin)

We measured the CTMin from June to Sept. 2005. We assigned individuals of each species to 3 temperature groups of 10, 20, and 30°C (*n* = 12-16 in each group). Each group of the same species contained lizards of approximately the same mean body weight. CTMin was measured after a 2 wk acclimation period at the assigned temperature with a 12: 12 h L: D photoperiod. Lizards were starved for 2 d prior to the CTMin measurements.

The CTMin is defined as the body temperature at which the animal loses its righting reflex (Hutchison 1961). To measure the body temperature, we inserted a thermocouple probe (K type, 0.1 mm in diameter) approximately 1 cm into the lizard's cloaca. The thermocouple probe connected to a data logger (RS-232, Thermolog 302, Center Technology Corp., Taiwan) was secured to the animal's tail with surgical tape. We measured the CTMin in a 0°C walk-in chamber. We put an experimental lizard into a test box (length x width x height of 17 x 10 x 10 cm). We used a light bulb (60 W) as a heat source to generate a thermal gradient. By gradually moving the lamp further away from the lizard, we decreased the lizard's body temperature by 0.6-0.9°C/min. Once the body temperature fell below 10°C, we checked the lizard's righting reflex every 30 sec by turning the lizard on its back and stimulating the pelvic region. If the lizard could not right itself within 1 min, its body temperature was recorded as the CTMin. Immediately after we obtained the CTMin, we placed the lizard in warm water (~25°C). All lizards recovered within a few min.

Survival rates under cold treatments

We carried out prolonged survival tests during the winters of 2004 and 2005. Before we recorded the survival rates of these 3 *Takydromus* species, lizards were kept in a temperature-controlled room at 25°C. For the experiment, we used temperatures of 2, 5, 10, and 15°C. Each treatment group contained lizards of approximately the same mean body weight (n = 16-17 for each treatment). Animals were individually housed in plastic boxes (length x width x height of 20 x 10 x 15 cm) containing dry soil, grass, and a tile shelter. They were put in incubators whose temperatures were decreased from 25°C to their assigned temperature settings at a rate of 1°C/d. Lizards were provided water and food (mealworms dusted with vitamin powder) *ad libitum* during the test, with a 12: 12 h L: D photoperiod. We recorded their survival state weekly.

To compare the experimental temperatures to field temperatures, we measured field temperatures at a high altitudinal plot (Kuanyuan, 2374 m in altitude) from Dec. 2004 to Mar. 2005. This plot was located in the natural range of *T. hsuehshanensis*. Soil temperatures of the surface (5 cm deep) and at a depth of 50 cm were recorded every 30 min with Hobo thermal data loggers (model H08-032-08, Onset Computer Corporation, Borne, MA, USA).

Data analysis

We used two-way analysis of variance (ANOVA) to analyze the effects of acclimation temperature and species on CTMin. The CTMin of lizards acclimated to 10°C was used as the lowest CTMin of these three species in the following tests. We compared the lowest CTMin values and their variances with the following hypotheses using the ordered heterogeneity (OH) test (Gaines and Rice 1990, Rice and Gaines 1994). The null hypothesis stated that the lowest CTMin values and their variances were equal among the three species, while the alternative hypothesis stated that the rank of the lowest CTMin and its variance was *T. hsuehshanensis* ≤ *T. formosanus* ≤ *T. stejnegeri* with at least one inequality strict. Differences in survival curves among these three species at each temperature treatment were examined by a Kaplan-Meier survival analysis (Kaplan and Meier 1958). All tests were conducted with the Statistical Package for Social Science (SPSS), version 13.0.

RESULTS

Critical thermal minimum (CTMin)

The CTMin was significantly affected by species ($F_{2,109}$ = 32.20, p < 0.001) and acclimation temperature ($F_{2,109}$ = 15.07, p < 0.001), but there were no interaction effects ($F_{4,109}$ = 1.41, p = 0.23). For the species effect, at all acclimation temperatures, *T. hsuehshanensis* had a significantly lower CTMin than did *T. stejnegeri* and *T. formosanus* (both p < 0.001), but those of *T. stejnegeri* and *T. formosanus* did not significantly differ (p = 0.76). For the temperature acclimation effect, the CTMin values of these *Takydromus* lizards were significantly higher at 30°C than at 10 or 20°C, but they did not significantly differ between 10 and 20°C treatments (Fig. 1).

The lowest CTMin and its variance of these lizards had the following rank: *T. hsuehshanensis*

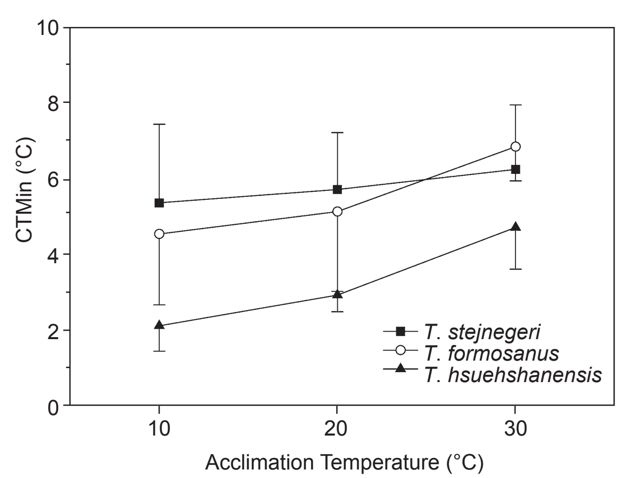

Fig. 1. Critical thermal minimum (mean ± 1 standard deviation) of three *Takydromus* lizards at 3 acclimation temperatures. Sample sizes for *T. stejnegeri*, *T. formosanus*, and *T. hsuehshanensis* were 16, 12, and 12, respectively.

(mean ± 1 standard deviation (SD) = 2.0 ± 0.7°C) ≤ *T. formosanus* (4.5 ± 1.9°C) ≤ *T. stejnegeri* (5.0 ± 2.1°C) (CTMin: ANOVA test, $F_{2,39}$ = 18.40, p < 0.001, OH test: rsPc > 0.99, p < 0.001; CTMin variance: Levene's test, $F_{2,37}$ = 5.03, p = 0.01; OH test: rsPc = 0.88, p < 0.02).

Survival rates during cold treatments

The survival curves of these 3 *Takydromus* lizards significantly differed at 2 and 5°C, but not at 10 and 15°C (both p > 0.50) (Fig. 2). At 2°C, *T. hsuehshanensis* had a significantly different survival curve from those of the *T. formosanus* and *T. stejnegeri* (both p < 0.001), but the survival curves of the latter two species did not significantly differ (p = 0.90). At 5°C, survival curves of *T. hsuehshanensis* and *T. formosanus* significantly differed from that of *T. stejnegeri* (both p < 0.01), but they did not significantly differ from each other (p = 0.89).

The temperatures recorded at the Kuanyuan plot are shown in figure 3. Most of the time, temperatures of the soil at 50 cm underground were higher than 5°C with the exception of 2 consecutive days. The lowest temperatures were 1.8 and 3.9°C at the surface and 50 cm underground, respectively. It is clear that the 2 and 5°C treatments in the laboratory experiment were much more rigorous than the temperature of 50 cm underground in the field at high altitude.

DISCUSSION

We found a significant acclimation temperature effect on the CTMin values of these three *Takydromus* lizards, which is consistent with

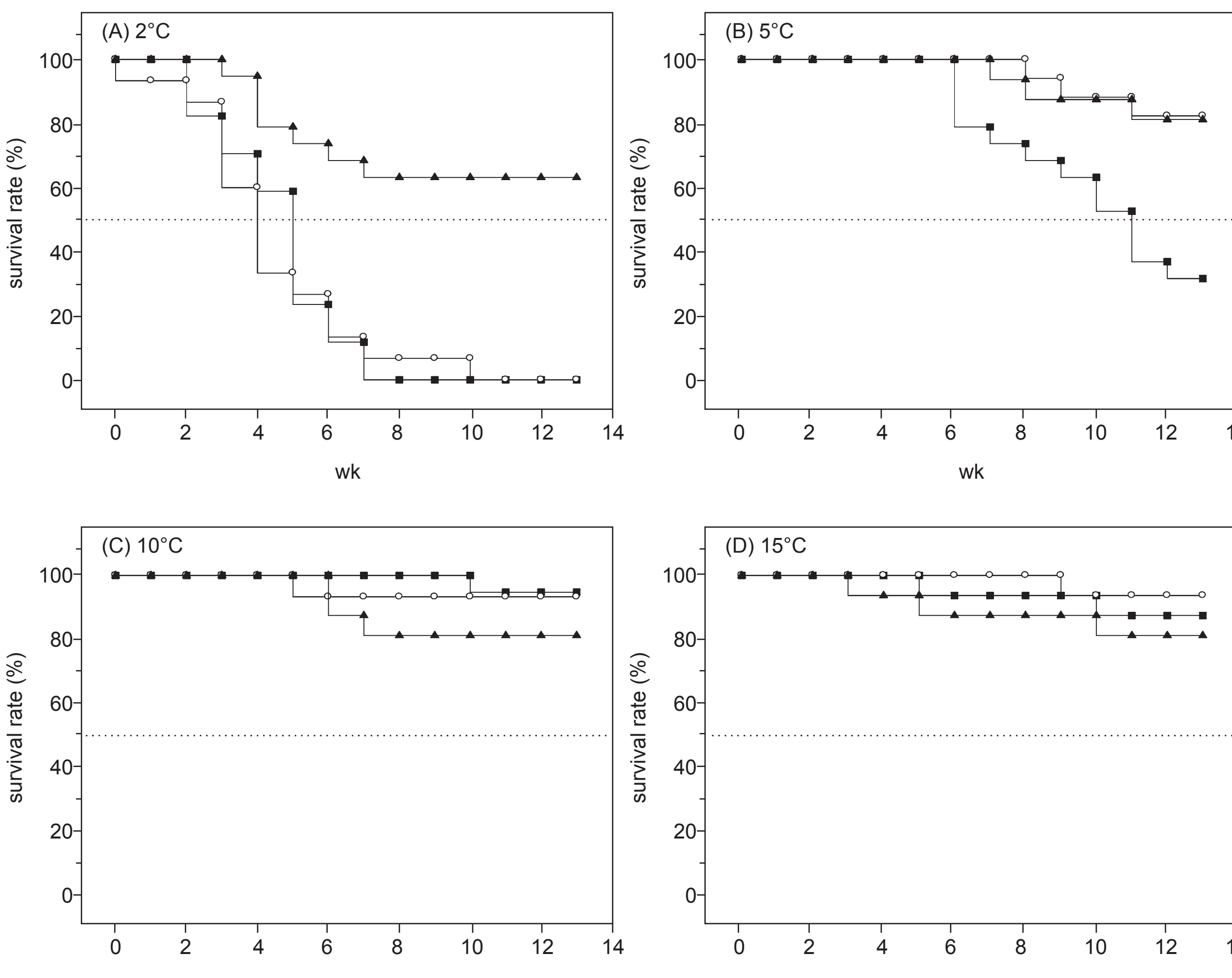

Fig. 2. Survival curves for *Takydromus stejnegeri* (■), *T. formosanus* (○), and *T. hsuehshanensis* (▲) at 4 different temperature treatments. The sample size for each species in each treatment was 16 or 17.

many previous studies on ectotherms (Lowe and Vance 1955, Hutchison 1961, Brattstrom 1968, Jacobson and Whitford 1970, Kour and Hutchison 1970). In this study, we took the CTMin at 10°C as the lowest CTMin for further comparison because CTMin values for each species at 10°C did not significantly differ from those of lizards at 20°C (Fig. 1). Because CTMin was correlated with altitudinal distribution in 3 lizards and because a comparative low variation of CTMin was found in *T. hsuehshanensis*, we suggested that the cold temperature was a strong selection factor in high altitude. It seemed that the CTMin should be correlated to relevant physiological traits that directly affected survivorship, but it was not itself directly important to the survivorship of these 3 species.

As predicted, we detected a positive correlation between cold tolerance and the altitudinal distributions of these 3 species. This finding is also consistent with previous studies that have showed a lower CTMin in ectothermic tetrapods living in cooler environments, such as higher altitudes (amphibians: Stuart 1951, Brattstrom 1968; reptiles: Spellerberg 1972a, Huang et al. 2006) or latitudes (amphibians: Brattstrom 1968; reptiles: Wilson and Echternacht 1987). However, some studies did not detect the same pattern among populations of a single species (Gvoždík and Castilla 2001) or among closely related species of reptiles living at different altitudes (Huang et al. 2007).

Although cold tolerance was highly correlated to the altitudinal distributions of these species, it was not a critical factor limiting the current altitudinal distributions of *T. formosanus* and *T. stejnegeri*. The lowest CTMin values of these 2 related species were between 4.5 and 5.0°C. At 5°C, 80% of individuals survived at least 6 wk. Even at 2°C, more than 60% of individuals survived for at least 4 wk (Fig. 2). Although the surface temperature at the high altitude (2374 m in altitude) fell below 2°C in winter, the soil temperature 50 cm underground exceeded 5°C most of the time with only the exception of 2 consecutive days (Fig. 3). Obviously, the low temperatures we observed at

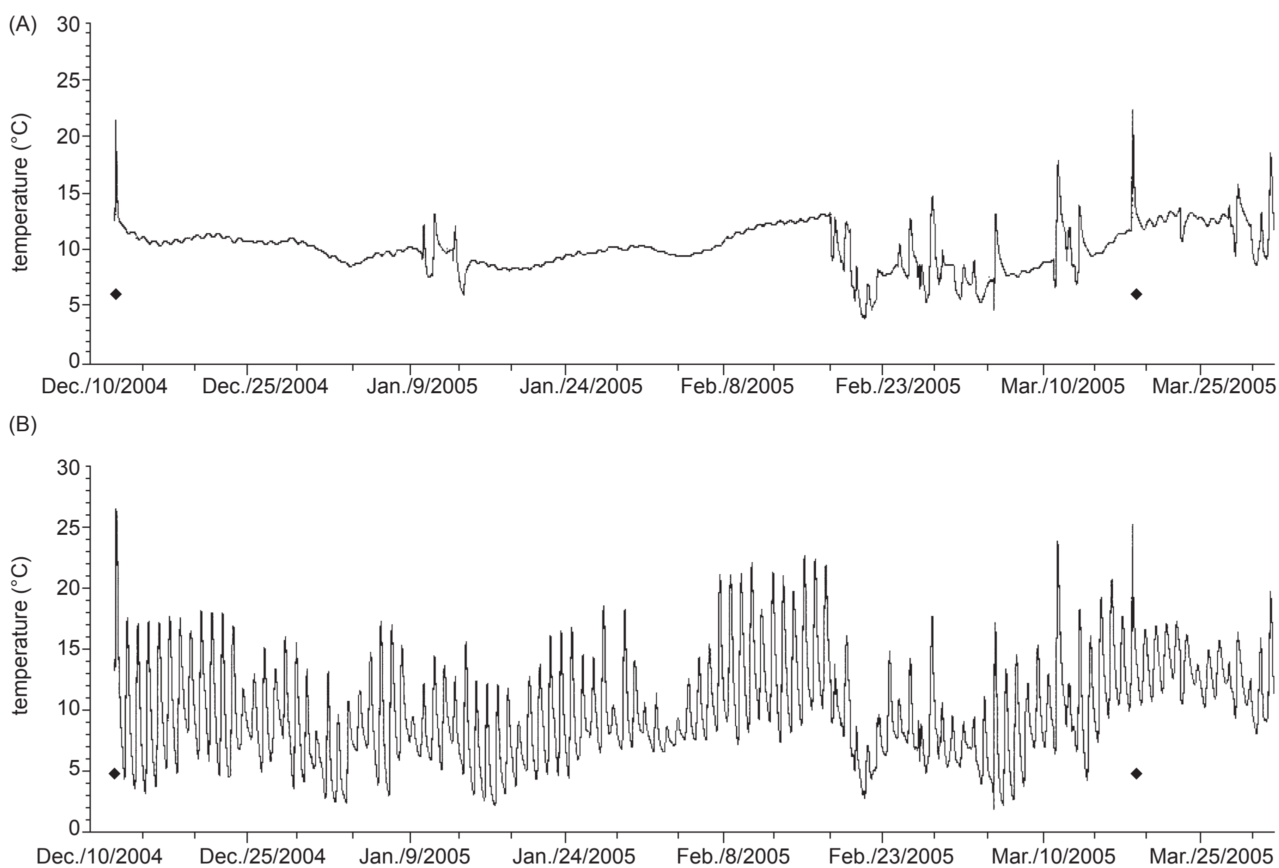

Fig. 3. Temperature recordings at Kuanyuan (2374 m in altitude) from Dec. 2004 to Mar. 2005. Surface temperature (A) and 50 cm underground (B) Diamonds indicate when the laptop was connected to the temperature data logger in order to launch the recordings at the beginning and to read out the data during the measurement period, respectively.

the high altitude would not freeze all individuals of these lizards. Therefore, if these 2 species are capable of moving to high altitudes, at least some individuals might survive the winter. In addition, we found the CTMin values of these 2 species did not significantly differ from that of another high-mountainous lizard, the Taiwanese skink (with a CTMin of 5.3°C, Huang et al. 2006). Therefore, cold temperatures at high altitude did not cause the deaths of these two species acutely or chronically.

The original concept of critical body temperature (i.e., CTMin and CTMax) is the body temperature at which an animal's locomotor activity becomes disorganized, and presumably it can no longer escape from conditions that will promptly lead to its death (Cowles and Bogert 1944, Lowe and Vance 1955, Hutchison 1961). This concept may be fine for CTMax, but might not be proper for CTMin. For instance, in our previous study, we found that these 3 *Takydromus* species would die when they reached the CTMax during the CTMax test if we did not immediately cool them (Huang and Tu 2008). In contrast, in the present study, these three species had high proportions of individuals that could survive at temperatures much lower than their CTMin for quite a long time. Whether CTMin is a proper index of ecological death merits further studies.

Although cold temperatures at high altitudes did not have a lethal effect on *T. formosanus* and *T. stejnegeri*, they could still have a negative effect on their altitudinal distribution. Based on the temperatures measured at a high altitude (3005 m; Endemic Species Research Institute, Taiwan), the monthly lowest air temperatures in the active season (May-Oct. 2005 and 2006) were between 1.9-4.2°C. When comparing these with the CTMin of *T. hsuehshanensis* (2.0°C) and that of the other two species (4.5-5.0°C), it is apparent that the 2 lowland, but not the high-mountainous, species may frequently encounter immobilizing situations at high altitude. Even if *T. formosanus* and *T. stejnegeri* are not immobilized, environmental temperatures may still affect their distributions by altering behavioral performances. In fact, it was reported that tropical lowland frogs lost their normal locomotor capacity at low temperatures normally occurring in high-mountainous areas (Navas 1996 2003). The locomotor performance of ectotherms is prominently affected by body temperature (Bennett 1980, van Berkum 1988) and it crucially impacts a reptile's survival in the field (Christian and Tracy 1981, Jayne and Bennett 1990). We assumed that if the 2 lowland species exhibit relatively poor performances at cold temperatures, they may have decreased abilities to compete for resources with the native high-mountainous species, and/or suffer higher mortalities from predation. Further investigations on the thermal performances of these 3 species are needed to examine the role of temperature on their altitudinal distributions.

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