

Thermal Tolerance and Altitudinal Distribution of Three *Trimeresurus* Snakes (Viperidae: Crotalinae) in Taiwan

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Szu-Mien Huang, Shu-Ping Huang, Yi-Huei Chen, and Ming-Chung Tu (2007) Thermal tolerance and altitudinal distribution of three *Trimeresurus* snakes (Viperidae: Crotalinae) in Taiwan. *Zoological Studies* 46(5): 592-599. We measured and compared the acute thermal tolerances of a high-altitude pit viper, *Trimeresurus gracilis*, with that of its lowland congeners, *T. mucrosquamatus* and *T. s. stejnegeri*, to test whether their thermal tolerances are limiting factors determining their altitudinal distributions. The critical body temperatures, both the summer critical thermal maximum (CTMax) and the winter critical thermal minimum (CTMin), of these 3 species were measured after 2 wk of acclimation at 3 temperature regimes (10, 20, and 30°C). We discovered that (1) both the CTMin and CTMax of these 3 *Trimeresurus* snakes increased with increasing acclimation temperatures; (2) the lowest CTMin values of *T. gracilis* and *T. mucrosquamatus* did not significantly differ from each other, and both of them were significantly higher than that of *T. s. stejnegeri*; and (3) the CTMax values of these 3 *Trimeresurus* snakes did not significantly differ from each other. Overall, we did not find a clear relationship between acute thermal tolerances and altitudinal distributions of these 3 *Trimeresurus* species; hence, their acute thermal tolerances should not be limiting factors in determining their altitudinal distributions. <http://zoolstud.sinica.edu.tw/Journals/46.5/592.pdf>

Key words: Pit viper, Critical thermal maximum, Critical thermal minimum, altitude, Temperature.

Taiwan, a mountainous island off the eastern fringe of the Asian mainland, is located on the continental shelf and rises to an elevation of nearly 4000 m. It became an island approximately 4 million yr ago and has been connected to the continent more than once since its emergence (Hsu 1990). Kano (1940) postulated that the animal fauna in Taiwan came from 2 different zoogeographic regions, the Paleoarctic and Oriental areas. During various glacial epochs, Paleoarctic animals migrated to Taiwan. When the glaciers receded and temperatures in lowland areas increased, these animals retreated to mountainous areas. At the same time, Oriental animals came in and colonized lowlands through the land bridge that connected the Asian continent and Taiwan. The well-known glacial relict species, *Hynobius*, a salamander, is a typical example in Taiwan. It belongs to the Paleoarctic animal element but

nowadays is restricted to high mountainous areas (Lue and Chen 1989). In a similar way, several species of rodents with different altitudinal distributions were also found to be the result of 2 separate incursions during land-bridge connections (Yu 1995).

Since body temperature greatly impacts physiological functions and behavioral performances of ectothermic animals (Bennett 1980, Kaufmann and Bennett 1989, Angilletta 2001), differences in altitudinal distributions of animals might be related to their thermal physiological characteristics, such as thermally related performances or tolerances. Ectotherms usually do not have autonomic mechanisms of thermoregulation seen in endotherms and have to rely on selecting and shuttling between appropriate thermal microhabitats to acquire and maintain appropriate/desirable body temperatures (Swan 1952, Spellerberg 1972a,

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Huey and Pianka 1977, Hertz and Huey 1981, Avery 1982, Huey 1982). Although ectotherms are capable of behaviorally regulating their body temperatures, their physical environments eventually limit the extent of their thermoregulation (Huey 1974, Huey and Stevenson 1979, Wu and Kam 2005). It is therefore expected that the survival of ectotherms is greatly impacted by the ambient temperatures of their habitats. Some researchers consider ambient temperatures to be the most important environmental factor limiting the distribution of reptiles (Campbell and Solorzano 1992). Because of the strong association between environmental temperature and body functions of reptiles, their thermal tolerances may be well correlated with the temperatures of their habitats and with their geographic distributions (Jacobson and Whitford 1970, Kour and Hutchison 1970, Graham et al. 1971, Spellerberg 1972b, Greer 1980). For instance, the cold tolerance of the sea snake, *Pelamis platurus*, might be a physiological constraint influencing its latitudinal distribution (Graham et al. 1971). Also, the heat tolerance of *Sphenomorphus* skinks in the Australian continent is related to their different thermal habitats as well as geographic distributions (Greer 1980).

In this study, we focused on the relationship between the thermal tolerances and altitudinal distribution of 3 *Trimeresurus* pit vipers in Taiwan. The Taiwan mountainous pit viper, *T. gracilis*, is an endemic snake which only lives at altitudes above 2000 m, whereas, its 2 congeneric species (*T. mucrosquamatus* and *T. s. stejnegeri*) mostly inhabit low-elevation areas (Lue et al. 1999). The ambient temperature decreases with elevation at an approximate rate of 5.4°C/km (Su 1984). Thus, the mean temperature difference between areas at 3000 m and lowland areas might be up to 15°C. We hypothesized that the ambient temperature is one of the factors that prevents these 3 species of snakes from expanding their ranges of distribution. For instance, the mountainous *T. gracilis* should be capable of tolerating colder mountain temperatures, but it might not be able to tolerate the heat of lowland areas. On the other hand, the 2 lowland species should be capable of tolerating the heat of lowland areas, but they might not be capable of tolerating cold mountain temperatures. We investigated the acute thermal tolerances of these 3 species to test whether their thermal tolerances corresponded to their specific altitudinal distributions. For each species, we measured and compared the critical thermal minimum (CTMin) and critical thermal maximum (CTMax).

Since an acclimation temperature effect on CTMin and CTMax has been reported in many studies (Brattstrom and Regal 1965, Brattstrom 1970 1971, Hutchison and Ferrance 1970, Hutchison and Rowland 1974), we measured each species' CTMin and CTMax after 2 wk acclimation at 3 temperature regimes (10, 20, and 30°C). A seasonal effect can also influence the cold tolerance (Joy and Crews 1987, Layne 1995) and heat tolerance (Feder and Pough 1975, Lucas and Reynold 1967, Spellerberg 1972a) of ectotherms. Thus, we measured the CTMax and CTMin during both summer and winter. However, since the summer CTMax and winter CTMin have greater ecological importance than the winter CTMax and summer CTMin, we only examined the relationship between altitudinal distributions of these 3 *Trimeresurus* pit vipers with their summer CTMax and winter CTMin values in this paper. Whether seasonal changes in thermal tolerances occur in these snakes is discussed elsewhere. In this study, we expected that (1) values of CTMin and CTMax would be lower in *T. gracilis* than in the other 2 species, (2) values of the CTMin of *T. mucrosquamatus* and *T. s. stejnegeri* would be a limiting factor that prevents them from inhabiting mountainous areas, and (3) the CTMax of *T. gracilis* might restrict its distribution to mountainous areas.

MATERIALS AND METHODS

Experimental animals

The Taiwan mountain pit viper, *T. gracilis*, is viviparous and has a small body length (< 60 cm). It only inhabits mountainous areas above 2000 m (Lue et al. 1999). It is a rare, endemic, and protected species in Taiwan. In the wild, it frequently retreats under rocks during the daytime. The 2nd species, *T. mucrosquamatus* (body length < 150 cm), lives in lowland areas of Taiwan, and its geographic distribution includes Southwest China, Taiwan, the Indochina Peninsula, and India. In Taiwan, it can be seen in forest and agricultural areas below 1600 m. The 3rd species, *T. s. stejnegeri* (body length < 90 cm) is an arboreal snake, whose altitudinal distribution extends to mountainous areas up to 2000 m. Both *T. mucrosquamatus* and *T. s. stejnegeri* are nocturnal. In this study, we only collected snakes from the lowland populations of *T. mucrosquamatus* and *T. s. stejnegeri* to examine their thermal tolerances.

Animal collection

From 1998 to 2002, we collected *T. gracilis* ($n = 33$; males: snout-vent length (SVL) = 38.9 ± 1.2 cm SE, $n = 15$; females: SVL = 43.8 ± 1.4 cm SE, $n = 18$) from mountainous areas (> 2000 m) around the island (Nantou, Hsinchu, Kaoshiung and Taitung). Some adult *T. gracilis* born in our laboratory were also used in this study ($n = 15$, males: SVL = 33.5 ± 1.2 cm SE, $n = 9$; females: SVL = 35.7 ± 1.5 cm SE, $n = 6$). Individuals of *T. mucrosquamatus* ($n = 37$; males: SVL = 83.8 ± 2.8 cm SE, $n = 18$; females: SVL = 87.8 ± 3.2 cm SE, $n = 19$) were collected from Taipei, Miaoli, Taoyuan, Haulien, Nantou, and Taitung. Individuals of *T. s. stejnegeri* ($n = 46$; males: SVL = 50.6 ± 0.9 cm SE, $n = 27$; females: SVL = 55.0 ± 1.1 cm SE, $n = 19$) were collected from Taipei and Miaoli. After these snakes were taken back to the laboratory, they were individually housed in plastic boxes (length x width x height = $20 \times 12 \times 16$ cm) containing dry grass and a wood shelter for more than 1 month before the experiment. Water was provided at all times, and food (mice, and lizards) was provided approximately once every other week. Body weight was regularly monitored and was used as one of the health indicators. Unhealthy snakes were excluded from the experiment.

Experimental procedures

Snakes of each species were randomly assigned to one of 3 acclimation temperature regimes of 10, 20, and 30°C, while controlling for body size and sex ratio. The photoperiod was set to 12: 12 h L: D. The thermal tolerances of the snakes were measured in the summer (June-Sept. 2001 and June 2002) and winter (Dec. 2001-Mar. 2002). Each individual was acclimated at its assigned temperature regime for 2 wk prior the CTMin or CTMax measurement. Afterwards, it was put back into its box and acclimated for another 2 d at its originally assigned temperature before we measured the other critical body temperature.

To measure a snake's thermal tolerance, we used the critical thermal temperature or "dynamic method" as described by Lutterschmidt and Hutchison (1997a). Our studies were conducted in a walk-in chamber (length x width x height = $3.3 \times 2.6 \times 2.4$ m). The temperature inside the walk-in chamber was set to the acclimation temperature of that snake and then decreased or increased by 0.1-0.4°C/min. To measure the body temperature

of a snake, we inserted a thermocouple probe (K type, 30-gauge), connected to a data logger (RS-232, Thermolog 302, Center Technology Corp., Taiwan), 3-5 cm into its cloaca and secured it to the tail with surgical tape.

For the CTMin, we used the "loss of righting reflex (LRR)" as the behavioral endpoint. Since these 3 species are poisonous, we designed plastic boxes (for *T. gracilis* and *T. s. stejnegeri*: length x width x height = $50 \times 25 \times 7$ cm; for *T. mucrosquamatus*: length x width x height = $50 \times 25 \times 8$ cm) to observe their behaviors and to check their righting reflex during the heating and cooling processes (see details in figure 1). A snake was placed upside down, and when it did not immediately show a righting reflex, we checked it again by pinching its tail every 2 min. The body temperature at which the snake's LRR occurred was recorded as its CTMin. As soon as the CTMin was recorded, we put the test snake in 23°C water to warm it up. Most of the tested snakes recovered within 5 min, but a few died ($n = 3$).

For CTMax, we used the "gaping event" as the behavioral endpoint. Although Lutterschmidt and Hutchison (1997b) recommended that the sudden "onset of muscular spasms" is a better end point for CTMax, we found it difficult to observe that in these snakes. Once a snake began to exhibit gaping behavior during the heating process, it would frequently wriggle upside down and soon stop moving. Therefore, the gaping event of the snake could be regarded as the onset of the LRR in heat stress. We thus defined the body temperature at which the tested snake showed the "gaping event" as its CTMax. As soon as the CTMax was recorded, we put the snake in 23°C water to cool it. Most of the snakes recovered within 10 min, but a few took longer than 10 min to recover and a few eventually died ($n = 5$).

Data analysis

Before we lumped the critical body temperature data (i.e., the CTMin or CTMax) of *T. gracilis* snakes that were born in the laboratory with the data from snakes collected in the field into the analysis, we examined whether their critical body temperatures significantly differed using the Mann-Whitney Wilcoxon test. The data were first subjected to Levene's test for homogeneity of variance. A Kolmogorov-Smirnov test was performed to test the normality of the data residuals. We analyzed the data in 2 ways. First, we used a two-

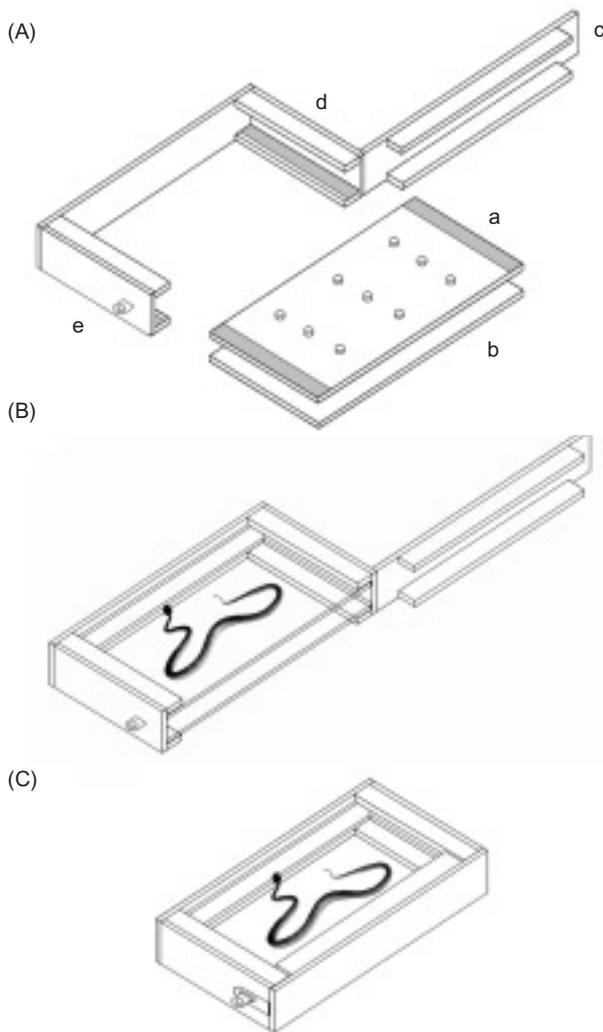


Fig. 1. Righting reflex testing box, a rectangular transparent plastic box. (A) Illustration of its removable top (a) and bottom (b) plates, with tiny holes for aeration. The 3 fixed lateral sides serve to hold the removable plates on the top and bottom, while the 4th lateral side (c) serves as a door. The left and right fixed lateral sides (d, e) present 2 holder edges each, with a Velcro strip (shown in gray) which was glued on both inner sides along their entire lengths. The top and bottom removable plates also have Velcro strips (length x width = 25 x 3 cm) glued to the right and left edges of their outward sides only. (B) Illustration of how the removable plates are inserted through the door, and adhere to the box's edges using the Velcro strips. To test the critical body temperatures, we introduced the snake into the space between the top and bottom plates, then closed the side door and locked it, as shown in (C). We held the box with both hands on the left and right sides, and used our thumbs to gently press down on the upper plate. This action detaches the upper plate from the Velcro and locks the snake in place. While still pressing the upper plate, we turned the box upside down. Once upside down, we released the upper plate (now at the bottom). The top plate immediately falls back to its original position because of gravity, thus releasing the snake inside the box. At this moment the snake is free to perform its righting reflex.

way analysis of variance (ANOVA) with species and acclimation temperature as the 2 main effects. If a significant interaction between species and acclimation temperature was detected, a post-hoc simple main-effects method (Becker and Coolidge, 1991) was used to assess the effect of acclimation temperature on critical body temperatures of each species and to examine whether the critical body temperatures differed among these 3 species at each acclimation temperature. Significant simple main effects of acclimation temperature or species were further analyzed using pair-wise comparisons. In order to maintain an overall α level of 0.05, a Bonferroni method was used to adjust the α level to 0.005 ($= 0.05/9$) for each comparison. Second, we used the ordered heterogeneity test (OH test, Gaines and Rice 1990, Rice and Gaines 1994) following 2 hypotheses: the null hypothesis stated that the mean of the critical body temperatures was equal among the 3 species, while the alternative hypothesis stated that the means of the critical body temperatures were in the order of *T. mucrosquamatus* \geq *T. s. stejnegeri* \geq *T. gracilis* with at least one inequality strict. Data of the critical body temperatures are presented as the mean \pm 1 standard error (SE) (with the 95% confidence interval (CI)). All tests were performed using the Statistical Package for the Social Sciences (SPSS) statistical software, version 13.0 (SPSS institute).

RESULTS

Critical thermal minimum (CTMin)

As a comparison of CTMin data between laboratory-born and field-collected *T. gracilis* revealed no significant differences (all $p > 0.05$, Mann-Whitney Wilcoxon test), we lumped these data together for further analyses. The ANOVA results indicated there were significant effects of species, acclimation temperature, and their interactions on the CTMin of these *Trimeresurus* snakes (see ANOVA results in table 1). In figure 2, the non-parallel lines indicate a significant interaction between species and acclimation temperature effects. We found that the CTMin of *T. mucrosquamatus* significantly increased when the acclimation temperature increased from 10 to 30°C (all $p < 0.001$), while the CTMin of the other 2 species significantly increased only when the acclimation temperature changed from 20 to 30°C (all $p < 0.001$), but not from 10 to 20°C (*T.*

gracilis, $p = 0.01$, *T. s. stejnegeri*, $p = 0.15$) (also see Fig. 2). A significant difference in CTMin values among species was detected at the acclimation temperatures of 10 and 20°C, but not of 30°C. At 10°C acclimation, the CTMin values of both *T. gracilis* and *T. mucrosquamatus* were significantly lower than that of *T. s. stejnegeri* (both $p < 0.0001$), but they did not significantly differ from each other. At 20°C acclimation, only the CTMin of *T. gracilis* was significantly lower than that of *T. s. stejnegeri* ($p < 0.001$), while the CTMin of *T. mucrosquamatus* did not significantly differ from that of *T. gracilis* ($p = 0.03$) or that of *T. s. stejnegeri* ($p = 0.52$) (also see Fig. 2). At 10°C acclimation, these snakes had the lowest CTMin values, which were $3.7 \pm 0.2^\circ\text{C}$ (95% CI: 3.2-4.2°C), $3.5 \pm 0.2^\circ\text{C}$ (95% CI: 2.9-4.1°C), and $5.6 \pm 0.2^\circ\text{C}$ (95% CI: 5.0-6.1°C) for *T. gracilis*, *T. mucrosquamatus*, and *T. s. stejnegeri*, respectively.

Critical thermal maximum (CTMax)

The CTMax value of laboratory-born *T. gracilis* (median = 39.6°C, $n = 3$) significantly differed from that of snakes collected from the field (median = 38.7°C, $n = 6$) in the 30°C acclimation treatment ($p = 0.02$, Mann-Whitney Wilcoxon test), but not in the other treatments ($p > 0.2$). Thus, we discarded the data collected from laboratory-born snakes in the 30°C treatment and lumped those collected from the other 2 temperature treatments together. The CTMax of these 3 species were significantly affected by the acclimation temperature effect ($F_{2,84} = 10.3$, $p < 0.001$), but not by the species effect (ANOVA test: $F_{2,84} = 0.97$, $p = 0.38$; OH test: $r_s P_c = 0.31$, $0.12 < p < 0.24$) or their interactions ($F_{4,84} = 0.35$, $p = 0.84$). Post-hoc analysis showed that the CTMax values of these *Trimeresurus* snakes significantly increased when the acclimation temperature changed from 20 to

30°C ($p = 0.002$), but not from 10 to 20°C ($p = 0.99$) (also shown in Fig.3). At 30°C acclimation, these snakes had the highest CTMax values, which were $38.3 \pm 0.3^\circ\text{C}$ (95% CI: 35.5-39.0°C), $38.6 \pm 0.3^\circ\text{C}$ (95% CI: 38.0-39.2°C), and $38.9 \pm 0.3^\circ\text{C}$ (95% CI: 38.3-39.4°C) in *T. gracilis*, *T. mucrosquamatus*, and *T. s. stejnegeri*, respectively.

DISCUSSION

We found that acclimation temperatures had a significant impact on both the CTMin and the CTMax of these 3 *Trimeresurus* species. These results are consistent with many previous studies that have found acclimation temperatures to be an important factor for both the CTMin and CTMax of ectotherms (e.g., salamanders, Hutchison 1961; anurans, Brattstrom and Lawrence 1962, Brattstrom 1968; lizards, Lowe and Vance 1955,

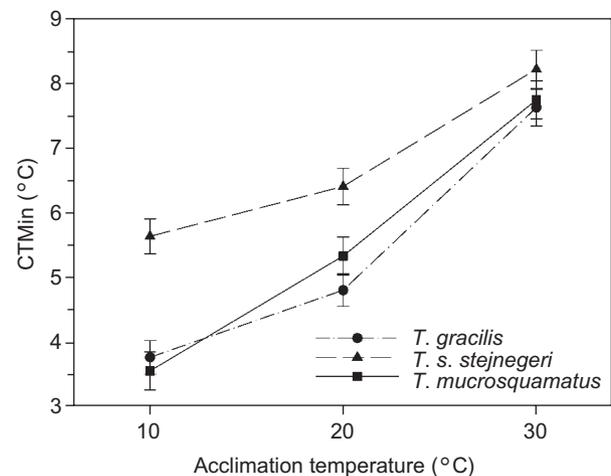


Fig. 2. Critical thermal minimum (CTMin, estimated marginal mean \pm 1 standard error bar) of *Trimeresurus gracilis* ($n = 41$), *T. s. stejnegeri* ($n = 36$), and *T. mucrosquamatus* ($n = 33$) in the 3 acclimation temperature regimes.

Table 1. ANOVA results for the effects of species and temperature on the critical temperature minimum (CTMin) of 3 *Trimeresurus* species

Source of variance	Sum of squares	d.f.	Mean squares	F ratio
Species	40.35	2	20.17	21.31***
Temperature	229.06	2	114.53	121.00***
Species x temperature	9.37	4	2.43	2.57*
Error	95.60	101	0.95	
Total	375.90	109		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Kour and Hutchison 1970, Corn 1971, Patterson 1999; and snakes, Jacobson and Whitford 1970).

We postulated that both the CTMin and CTMax values of the high-mountain snake, *T. gracilis*, should be lower than those of its 2 lowland congeneric species. However, the results did not support our prediction. For ectotherms widely distributed along altitudinal ranges, higher-altitudinal populations may have different thermal tolerances compared to those of lower altitudinal populations. For example, in 2 species of *Anolis* lizards, *A. semilineatus* and *A. gundlachi* (Hertz 1979, Hertz et al. 1979), the CTMax values of the higher altitudinal populations were lower than those of the populations living in lower altitudes. On the other hand, significant correlations between critical body temperatures (i.e., CTMin and CTMax) and altitudinal distributions could not be detected in other species. For instance, Hertz and Nevo (1981) found that thermal limits did not vary among different altitudinal populations of an agamid lizard, *Stellio stellio*. Similar results were observed in 2 species of skinks, *Sceloporus undulates* (Crowley 1985) and *Mabuya striata* (Patterson 1999), and a lacertid lizard, *Zootoca vivipara* (Gvoždík and Castilla 2001).

We found the lowest mean CTMin of *T. mucrosquamatus* (3.5°C) was not significantly lower than that of *T. gracilis* (3.7°C), indicating that its CTMin should not be a limiting factor for its highland distribution. Although the lowest mean CTMin of *T. s. stejnegeri* (5.6°C) was significantly higher than that of the other 2 species, it still

should not be a limiting factor. We compared the lowest CTMin of *T. s. stejnegeri* to the temperature recordings at Tatchia, a mountain station (Long-term Ecological Research Meteorological Station, 2550 m in altitude), where *T. gracilis* can be observed. We found the lowest ground surface temperature was 1.9°C in the winters of 2001–2003. However, the measured temperatures at 0.3, 0.5, and 1.0m underground at the Tatchia station were 4.4, 5.0, and 6.9°C, respectively, on the coldest day (3 Jan. 2002). Therefore, lowland *T. s. stejnegeri* might survive underground as do *T. gracilis*. Similarly, the highest CTMax of *T. gracilis* was not significantly lower than that of the other 2 species. Thus, the CTMax should not be an important factor limiting its altitudinal distribution.

Contrary to our prediction, the critical body temperatures were not the limiting factor that restricted these 3 *Trimeresurus* snakes' altitudinal distributions. However, ambient temperatures may cause chronically deleterious effects on normal physiological functions of ectotherms and in turn affect their altitudinal distributions. For example in a previous study (Huang et al. 2006), we found that chronic thermal tolerance might be more important than acute tolerance in determining the altitudinal distributions of 2 *Sphenomorphus* lizards in Taiwan. In that case, the high-mountain skink, *S. taiwanensis*, was capable of tolerating temperatures as high as 38.6°C for a short period of time, but suffered high mortality when it was kept at a constant temperature of 30°C for a long period of time. Whether chronic deleterious effects of certain temperatures have a crucial impact on the distributions of these *Trimeresurus* snakes remains to be resolved.

Other than chronic deleterious effects of temperatures, environmental temperatures may limit their distribution ranges through other aspects of thermal physiology. For example, the locomotor performance has been shown to be prominently affected by body temperatures (van Berkum 1988) and to have crucial impacts on animals' survival in the field (Christian and Tracy 1981, Jayne and Bennett 1990). Also, thermal requirements of embryonic development may be related to the geographic distributions of snakes (Lourdais et al. 2004). Further investigations on the influences of temperatures on thermal performances and/or fecundity of these *Trimeresurus* snakes are needed to examine the role of temperature in their altitudinal distributions.

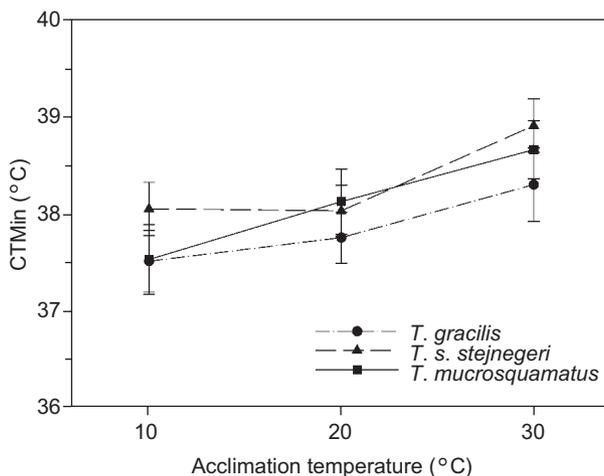


Fig. 3. Critical thermal maximum (CTMax, estimated marginal mean \pm 1 standard error bar) of *Trimeresurus gracilis* ($n = 28$), *T. s. stejnegeri* ($n = 37$), and *T. mucrosquamatus* ($n = 25$) in different acclimation temperature regimes.

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