
The Effect of Temperature and Thermal Acclimation on Locomotor Performance in *Xantusia vigilis*, the Desert Night Lizard

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Abstract

The influence of body temperature (12.5°–37° C) and thermal acclimation (20° and 30° C) on sprint speed in a thigmothermic lizard, Xantusia vigilis, was measured. Body temperature has a profound influence on sprint speed, which is maximal at 33°–34° C and declines exponentially at lower body temperatures. Neither sprint speed nor its thermal dependence was modified by thermal acclimation over the body temperature range of 15.0°–34° C. In contrast, acclimation temperature did affect sprint speed at more extreme temperatures: 20° C-acclimated lizards ran faster at 12.5° and slower at 37° C than did 30° C-acclimated animals. Acclimation also affected preferred body temperatures and critical thermal minima and maxima: all were significantly lower in the 20° C-acclimated group (31.1°, 4.5°, and 40.5° C, respectively) than in the 30° C-acclimated group (33.0°, 9.4°, 43.0°). Acclimation may therefore shift critical thermal variables without affecting locomotor performance at intermediate temperatures.

Introduction

Most ectotherms experience variation in body temperature in variable thermal environments. For many species of terrestrial ectotherms, daily and seasonal environmental temperatures fluctuate greatly. For example, desert lizard species in the American Southwest may experience daily changes in air temperature as great as 30° C and surface temperatures in excess of 60° C (Cowles and Bogert 1944). Ectotherms often ameliorate the physiological

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effects of variable thermal conditions by avoiding thermal extremes through behavioral thermoregulation. They may also make physiological and biochemical adjustments to thermally variable conditions (i.e., thermal compensation or acclimatization).

Although the importance of thermal compensation and acclimatization in natural populations remains unclear, the possibility of thermal compensation is particularly interesting because of the thermal dependence of locomotor performance capacity (see Bennett 1985 for a review). The reduction of sprint speed and stamina at low body temperatures may be especially significant for the behavioral capacity and survival of ectotherms (Putnam and Bennett 1981; Bennett and John-Alder 1984; Marsh and Bennett 1986). The role of thermal compensation in altering this basic pattern of thermal dependence of locomotor performance has been assessed for only a few species of vertebrate ectotherms. Studies of fish locomotion show effects of thermal acclimation on prolonged swimming speed (Fry and Hart 1948; Rome, Loughna, and Goldspink 1985). In contrast, most studies on amphibians have shown no significant effect of acclimation temperature on locomotor performance (Putnam and Bennett 1981; Renaud and Stevens 1981*a*, 1981*b*, 1983*a*, 1983*b*, 1984; Rome 1983; Else and Bennett 1987). An exception is recent work on the toad *Bufo woodhousii*, in which acclimation produced a significant effect on all four measures of locomotor performance, including mean jump distance and mean jump velocity (Londos and Brooks 1988). No previous studies have examined the effects of long-term temperature exposure on locomotor performance in reptiles.

The present study was conducted to determine the effects of thermal acclimation on the sprint locomotor performance of a thigmothermic desert lizard, *Xantusia vigilis vigilis* (the desert night lizard, family Xantusiidae), a small, secretive, ground-dwelling species occurring in arid and semiarid areas of the American Southwest. This species was chosen because it, unlike other syntopic species, is active throughout the year, and, as it does not bask in the sun, its body temperature approximates ground temperature, which ranges from 10°C in the winter to over 40°C in midsummer. Field active body temperatures have been reported to range between 11° and 29°C (Morafka and Banta 1973). At different times of the year, these animals must therefore experience and be active under a wide variety of body temperatures. These conditions suggest the potential importance of an acclimatory effect on locomotor ability in this species. These lizards are usually found in association with species of yucca (e.g., joshua tree, *Yucca brevifolia*) and can be occasionally found under dense brush, rock flakes, and cow droppings (Stebbins 1985). When exposed under natural conditions, animals

sprint rapidly for cover, and thus sprint performance may play an important role in predator avoidance in this species. To determine the effect of body temperature and thermal acclimation on performance parameters, we made quantitative measurements of sprint speed, preferred body temperature (PBT), and the critical thermal maximal (CTMax) and minimal (CTMin) temperatures for *Xantusia vigilis* acclimated to either 20° or 30° C.

Material and Methods

Acclimation of Experimental Animals

Thirty-two adult *Xantusia vigilis* (mixed sexes, mean mass = 1.4 g) with complete tails were collected from wood rat nests and fallen branches under Joshua trees (*Yucca brevifolia*) near Victorville, San Bernardino County, California, in September, 1987 (CA collecting permit 0986 to A.F.B.). Sixteen animals were randomly assigned to each of the two acclimation temperatures in different constant temperature chambers set at a constant 20° and 30° C (range = $\pm 1^\circ$ C). There was no significant difference in mean body mass of the acclimation groups (*t*-test, $P = 0.455$). A 12L:12D photoperiod was maintained using 40-W cool fluorescent tubes for the 50-d acclimation period prior to any experimental testing. All animals were fed fruit flies. Water was available ad lib. every other day. Body weights were taken within 48 h of the time of capture and the end of the acclimation period. If an animal lost more than 25% of its body weight during the acclimation period or dropped its tail while being manipulated, it was excluded from the analysis (no animals were excluded by the weight loss requirement, though five were excluded because of tail loss).

Maximum Sprint Speed

A track (175 cm long by 10 cm wide) inside a controlled temperature room was used for all sprint measurements. Photocells, installed at 25-cm intervals along the track, were set to be triggered by the head of a passing animal. The time between sequentially triggered photocells and the resultant sprint speed were determined by an IBM XT computer linked to the apparatus via a microprocessor (see Huey et al. 1981, for a general description of the apparatus). The floor of the track was covered with a sheet of pegboard (unfinished side up) to provide traction for the animal during the run. The walls of the track were made of smooth, paper-covered Plexiglas 25 cm high.

All animals were moved into the preset controlled temperature room 1 h

prior to testing. Each animal ran four trials on the sprint track, with 1 h recovery between trials. Animals from each acclimation group were alternated during each trial. Animals were initially prodded by hand at the beginning of each run. The fastest velocity over any 25-cm segment in any trial was recorded as the sprint speed at the experimental temperature. At the end of the daily trial period, animals were returned to their respective acclimation temperatures. Water was supplied during the test period, but not food.

Animals were run daily at the following sequence of temperatures: 30°C (day 1); 25°C (day 2); 20°C (day 3); 15°C (day 6); 34°C (day 7); 37.5°C (day 8); 12.5°C (day 9). Room temperature was maintained within a range of $\pm 0.5^\circ\text{C}$. All trials were run between 1500 and 2000 hours. Field observations suggest that *X. vigilis* is most active on the ground surface at this time.

Preferred Body Temperature

The preferred body temperature of each lizard was measured after the completion of the sprint trials. A darkened, 150 × 15-cm thermal gradient was used for all tests. The gradient consisted of a single copper plate with one end projected into an ice bath and the other end on a hot plate. A constant 5°–55°C temperature gradient (0.3°C/cm) was created after the temperature of the device stabilized. The gradient was divided lengthwise with a cardboard wall, permitting two isolated animals (one from each acclimation group) to be run simultaneously. After the animals were first placed in the center of the gradient, the gradient was covered with Plexiglas to minimize disturbance. After 1 h, the animals were removed and their body temperatures were quickly taken with a fast-reading thermocouple inserted through the cloaca. Care was taken not to alter the animal's temperature with handling. All tests were conducted between 1500 and 2000 hours.

Critical Thermal Minimum and Maximum

For determining the critical thermal minimum, a 20 × 30-cm plastic container was placed in an ice bath. The test animal was placed into the container and not handled until movement appeared sluggish. At this point, a very fine thermocouple (40 gauge) was inserted into the animal's cloaca and the animal was returned to the cooling container. The body temperature was monitored with a digital electronic temperature (Wescor TH-65 Digital TC Thermometer). A thin layer of insulating rubber was placed in the bottom of the container so that body temperature fell approximately 1.0°C/min below 15°C. The test animal was prodded approximately every minute and loco-

motor ability noted. The animal was flipped on its back, and the presence of a righting response was scored. The temperature at which the righting response was lost was taken as the CTMin. One measure of CTMin was taken for each test animal.

For the measurement of the CTMax, a thermocouple was inserted into the cloaca of the test animal. The animal was placed in a 20 × 25-cm steel open-topped container. A 300-W reflecting bulb was attached to a ring stand and placed directly over the test container. The height of the bulb was altered until the test animal experienced an increase in body temperature of approximately 1.0°C/min. The animal was prodded periodically during the course of the test, and its behavior was noted. As the animal approached its CTMax, its limbs became rigid and it waved the tip of its tail. As in the CTMin tests, the animal was periodically flipped and its righting response noted. The temperature at which righting response was lost was taken as the CTMax. The animal was then quickly dropped into cool water to prevent damage due to excessive heat. All animals successfully recovered after both critical thermal tests.

Analyses

To facilitate the comparison of the thermal dependence of locomotor performance between acclimation groups, we used a modified minimum polygon method to describe the general thermal dependence of the data (van Berkum 1986). The "optimal temperature range" (Huey and Stevenson 1979; Hertz, Huey, and Nivo 1983) for sprinting for each acclimation group was estimated by determining the range of performance temperatures at which each group maintained 95% (B_{95}) of maximal sprint speed. The midpoint of the 95% performance breadth was calculated as the "optimal" temperature (T_o) for sprint speed (Huey and Stevenson 1979; Hertz et al. 1983). The "tolerance range" was calculated as the difference between CTMax and CTMin (Huey and Stevenson 1979). The Q_{10} 's of speed for each acclimation group were calculated for the 10°C range below T_o and for each 5°C interval (Huey and Bennett 1987).

T-tests were done between acclimation groups for PBT, CTMin, and CTMax. The effects of body temperature, acclimation, and individual differences (among repeated runs) on the sprint performance were determined with a within-subjects repeated-measures ANOVA using SPSS (Norusis 1986) and subsequent paired *t*-tests on each performance temperature (significance as $P < 0.05$).

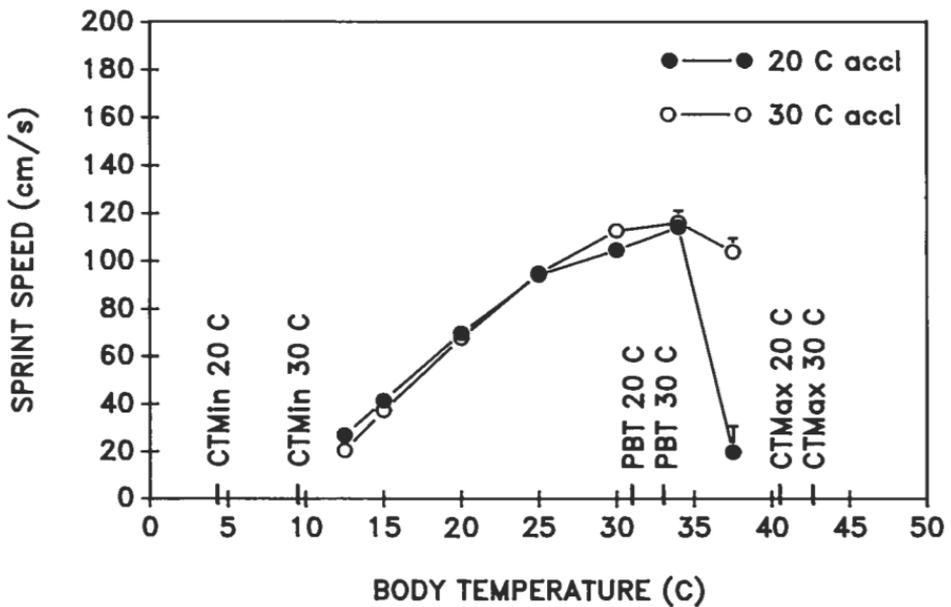


Fig. 1. Sprint speed and locomotor performance limits in *Xantusia vigilis* acclimated to 20° and 30° C. Error bars indicate SEs; dots may encompass error bars. Preferred body temperature and critical thermal minima and maxima are also reported.

Results

The Effects of Body Temperature and Acclimation on Sprint Speed

Sprint speed for each acclimation group is plotted against test temperature in figure 1. The thermal dependence of the performance curve for *Xantusia vigilis* is similar to that observed for many other lizard species and is neither translated nor rotated in a manner that would improve performance at lower body temperatures (Bennett 1980; Hertz et al. 1983; Huey et al. 1989). The Q_{10} values ranged from 5.63 (12.5°–15° C interval) to 1.29 (30°–34° C interval) for the 20° C acclimation group and 11.28 (12.5°–15° C interval) to 0.74 (34°–37.5° C interval) for the 30° C acclimation group (table 1). The Q_{10} 's for the temperature range of ($T_0 - 10$) to T_0 equaled 1.35 and 1.38 for the 20° and 30° C acclimation groups, respectively, and were similar to those observed for other lizards (R. B. Huey, F. H. van Berkum, A. F. Bennett, and P. E. Hertz, unpublished data). All sprint speeds within each acclimation group are significantly different from each other (paired t -test, $P < 0.002$), indicating that the effect of body temperature on performance was significant for all temperatures.

TABLE 1

*Q*₁₀'s for sprint performance for both acclimation groups

	Acclimation Group	
	20°C	30°C
12.5°–15°C	5.63	11.28
15°–20°C	2.77	3.30
20°–25°C	1.84	1.90
25°–30°C	1.25	1.19
30°–34°C	1.29	1.11
34°–37.5°C74
(<i>T</i> ₀ – 10)– <i>T</i> ₀	1.35	1.38

Note. *Q*₁₀ for the interval (*T*₀ – 10) to *T*₀ is based on the optimal temperature for sprinting (*T*₀) (see text for definition and method of calculation).

As is apparent from figure 1, acclimation had no effect on sprint performance over the range of body temperature of 15°–34°C. However, at 12.5°C, the 20°C acclimation group sprinted significantly faster (32%) than the 30°C acclimation group (*t*-test, *P* < 0.02). At 37.5°C, 13 of the 15 lizards of the 20°C acclimation group would not run, while all 12 animals of the 30°C acclimation group sprinted. We therefore performed two repeated-measures ANOVAs to analyze acclimation effects: one for body temperature range 15.0°–34°C and one for body temperature range 12.5°–37.5°C, assigning the nonperformers a speed of 0 cm/s (table 2). When the 12.5° and 37.5°C test temperatures are included in the repeated-measures ANOVA, the overall effect of acclimation on performance is highly significant (*P* < 0.001). However, when the 12.5° and 37.5°C test temperatures are excluded from the analysis, the overall effect of acclimation is not significant (*P* = 0.854). Clearly, acclimation in this experiment did not affect sprint performance over most of the normal thermal range of this species but only affected performance at temperatures approaching critical thermal limits. The overall effect of body temperature was also highly significant (*P* < 0.001), as suggested from the earlier statistical analysis.

There were also consistent differences among individuals in sprint performance (table 2), as has been noted in most other studies on locomotor performance (Bennett 1987). The fastest animal in this study ran 1.5 times the

TABLE 2

Results of repeated-measures analysis of variance analyzing the effects of body temperature, acclimation, and differences among individual animals on sprint speed

Body Temperature and Effect	F	df	P
15°–34°C (excluding 12.5° and 37.5°C):			
Body temperature	798.28	4	<.001
Acclimation temperature03	1	.854
Individual	12.05	25	<.001
12.5°–37.5°C:			
Body temperature	182.82	6	<.001
Acclimation temperature	8.66	1	<.01
Individual	4.04	25	<.001

speed of the slowest at moderate body temperatures. Sprint speed was not correlated with body mass ($P = 0.193$).

The Effects of Acclimation on Critical Thermal Limits and PBT

The effect of acclimation was significant for both CTMin and CTMax (t -test, $P < 0.001$) and PBT (t -test, $P < 0.03$) (table 3). All three temperatures are greater in the 30°C acclimation group. The optimal temperature range for sprinting of the 30°C acclimation group was 2.5°C greater than for the 20°C acclimation group, but the tolerance range (CTMax–CTMin) was 2.4°C smaller in the 30°C acclimation group.

Discussion

The thermal dependence of locomotor performance for *Xantusia vigilis* in this study is similar to that observed in other lizard species, including species with both high and low field body temperatures. These data are in agreement with the conclusion (Huey et al. 1989) that cold adaptation in nocturnal lizards does not include a shift in the thermal dependence of locomotor performance to lower temperatures, even though these animals may have PBTs as much as 5°C below those of diurnal lizards. Perhaps this shift in

TABLE 3

The effect of acclimation temperature on critical thermal values, preferred body temperature, and optimal temperatures

	Acclimation Temperature		P
	20°C (°C)	30°C (°C)	
Critical thermal minimum (CTMin)	4.5 ± .4 (10)	9.4 ± .3 (7)	<.001
Critical thermal maximum (CTMax) . . .	40.5 ± .2 (10)	43.0 ± .2 (8)	<.001
Tolerance range (CTMax-CTMin)	36.0	33.6	. . .
Preferred body temperature (PBT)	31.1 ± .5 (10)	33.0 ± .6 (8)	.033
Optimal temperature range (B_{95})	31.0-35.0	29.5-36.0	. . .
Optimal temperature (T_O)	33.0	32.8	. . .

Note. Mean values are reported with SEs; numbers of observations are in parentheses.

PBT in nocturnal species may be accompanied by other physiological functions that have their thermal optima at lower temperatures, in contrast to locomotor performance. Optimal temperature for sprinting coincides with preferred body temperature in *X. vigilis*.

The apparent lack of any effect of acclimation on the thermal dependence of sprint speed or on the absolute sprint speed for any temperature further supports a model of a fixed or "hardwired" basis for locomotor performance in lizards, unaffected by such factors as training or acclimation state (see Gleeson 1979; Garland et al. 1987). Similar data on amphibians are ambiguous. *Rana pipiens* was shown to exhibit some acclimation effects on jumping distance, but none were seen in *Bufo americanus* as reported in the same study (Renaud and Stevens 1983a) and in a study of acclimation of locomotor performance in the salamander *Ambystoma tigrinum* (Else and Bennett 1987). A recent study of *B. woodhousii* (Londos and Brooks 1988) found significant acclimation effects on four separate measures of locomotor performance. Data on fish suggest some effects of acclimation on endurance and cruising speed (Fry and Hart 1948; Larimore and Duever 1968; Griffiths and Alderdice 1972; Rome et al. 1985), but comparable studies on burst speed locomotor performance have not been undertaken.

Unlike the ambiguous results of effects of acclimation on locomotor performance, studies of muscle contractile properties in amphibians have

found no effects of acclimation (Renaud and Stevens 1981*a*, 1981*b*, 1983*b*, 1984; Rome 1983). In the study on *A. tigrinum*, no acclimation effect was observed in any of the seven isometric and isotonic muscle contractile properties measured, including peak twitch force, time to peak twitch force, and maximum isometric tension (Else and Bennett 1987). If sprint speed locomotor performance at low body temperatures in *Xantusia* depends directly on muscle contractile performance (as it does in some other lizards; see Marsh and Bennett 1986), it is unlikely that acclimation affects muscle contractile properties in *X. vigilis*.

The significant acclimation effect on the critical thermal limits and on the preferred body temperature is noteworthy, although the relationship between these factors and the thermal dependence of locomotion requires further discussion. Certainly the breadth of locomotor performance must lie completely within the limits set by the critical thermal maximum and minimum, but the thermal range over which locomotion is undertaken may be narrower. If the temperature difference between cessation of locomotion and loss of righting response is great (e.g., $>5^{\circ}\text{C}$), then the critical thermal limits per se probably have a minor role in defining the limits of locomotor performance. If, however, the temperature difference is narrow (e.g., $<2^{\circ}\text{C}$) then any shift in the critical thermal limits due to acclimation will affect a lizard's locomotor ability, at least at the extreme temperatures within its thermal niche breadth. For *X. vigilis*, the proximity of the critical thermal limits to locomotor limits may be responsible for the significant acclimation effect on performance at 37.5°C .

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